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Croissance et qualité organoleptique de la mangue (*Mangifera Indica*) : analyse expérimentale et modélisation de l'effet de la disponibilité hydrique et carbonée

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à Lucas .....

"La vie de famille, si douce et si précieuse ..."

Sommaire

INTRODUCTION **8**

1 Cadre général **9**

1.1 La maîtrise de la qualité, un enjeu pour la mangue 10

1.2 Le contexte agronomique 10

1.3 Le projet manguier à La Réunion 11

1.4 Objectifs et démarche de l'étude 11

2 Facteurs influençant la croissance et l'élaboration de la qualité **13**

2.1 Facteurs affectant la croissance du fruit 13

2.1.1 Alimentation carbonée *13*

2.1.2 Alimentation hydrique *14*

2.2 Elaboration de la qualité 15

2.2.1 Alimentation carbonée *15*

2.2.2 Alimentation hydrique *16*

3 La modélisation : outil d'étude du fonctionnement du fruit **18**

4 Plan du travail **20**

CHAPITRE I : MATERIELS ET METHODES **22**

1 Conditions et dispositifs expérimentaux **23**

1.1 Conditions expérimentales 23

1.1.1 Le site expérimental de la station du CIRAD-FLHOR à Bassin Plat *23*

1.1.2 Suivi des paramètres climatiques *23*

1.2 Dispositifs expérimentaux 24

1.2.1 Modification du rapport feuilles/fruit par décortication *24*

1.2.2 Variation de l'irrigation *25*

2 Mesures et analyses effectuées **26**

2.1 Caractérisation des organes sources 26

2.2 Caractérisation des organes puits 26

2.2.1 Etude de la croissance saisonnière des fruits *26*

2.2.2 Etude de la croissance horaire des fruits *27*

2.2.3 Etude de l'état hydrique des fruits *27*

2.2.4 Etude de la composition biochimique des fruits *28*

2.2.5 Etude du nombre de cellules à la fin de la croissance *28*

3 Analyses statistiques **29**

CHAPITRE II : EFFETS DE L'ALIMENTATION CARBONEE ET HYDRIQUE SUR L'ELABORATION DE LA QUALITE DE LA MANGUE **30**

1 Leaf-to-fruit ratio affects water and dry matter content in mango fruit. **32**

1.1 Introduction 33

1.2 Materials and methods 34

1.2.1 Material and treatments *34*

1.2.2 Data collection and analyses *34*

1.3 RESULTS 35

1.4 DISCUSSION 36

2 Leaf to fruit ratio and irrigation supply affect seasonal changes in minerals, organic acids, and sugars of mango fruits **38**

2.1 Introduction 40

2.2 Materials and methods 42

2.2.1 Experimental conditions and treatments *42*

2.2.2 Measurements of fruit composition *42*

2.2.3 Statistical analysis *44*

2.3 Results 44

2.4 Discussion and conclusion 46

2.4.1 Fruit composition and seasonal changes *46*

2.4.2 Assimilate and water supply affect fruit quality *47*

CHAPITRE III : ÉTUDE DU FONCTIONNEMENT CARBONÉ DE LA MANGUE : COMBINED EFFECTS OF CLIMATE AND SOURCE / SINK RELATIONS ON MANGO FRUIT GROWTH STUDIED BY A MODELLING APPROACH **50**

1 Introduction **54**

2 Materials and methods **57**

2.1 Plant material 57

2.2 Model Presentation 57

2.2.1 Carbon assimilation by leaves *58*

2.2.2 Fruit demand *59*

2.3 Measurements of fruit growth 60
2.4 Measurements for parameters assessment 60
2.4.1 Growth and maintenance respiration of fruit 60
2.4.2 Light saturated photosynthesis 62
2.4.3 Potential fruit growth and base temperature 62
2.4.4 Reserves mobilisation 63
2.4.5 Allometric relationships 64
2.4.6 Parameters taken from the literature 64
2.5 Model evaluation 64
2.6 Modelling Technique 64
2.7 Description of input data 65
2.8 Initial conditions 65
2.9 Description of a simulations used to assess the contribution of climate, initial fruit dry mass, and leaf-to-fruit ratio on fruit growth and underlying physiological processes 65
3 Results 67
3.1 Estimation of model parameters 67
3.2 Model test 68
3.3 Analysis of model sensitivity to parameters 69
3.4 Contribution of the effects of climate, initial fruit dry mass, and leaf-to-fruit ratio on fruit growth and underlying physiological processes 70
4 Discussion 71
4.1 Quality of adjustment and prediction of the model 71
4.2 How the initial fruit dry mass influences source/sink relationships? 71
4.3 How the leaf to fruit ratio influences source/sink relationships? 72
4.4 How the climate influences source/sink relationships? 73

CHAPITRE IV : ÉTUDE DU FONCTIONNEMENT HYDRIQUE DE LA MANGUE : AN ANALYSIS OF ELASTIC AND PLASTIC FRUIT GROWTH IN RESPONSE TO VARIOUS ASSIMILATE SUPPLIES 79
1 Introduction 83
2 Materials and methods 86

2.1 Plant material 86
2.2 Model presentation 86
2.3 Measurements for parameter assessment 90
2.3.1 Fruit surface conductance and hydraulic conductivity of xylem 90
2.3.2 Elastic modulus 91
2.3.3 Wall extensibility (ϕ), yield turgor pressure (Y) and conductivity (aL_p) 91
2.3.4 Allometric relationships 92
2.3.5 Parameters of the proportions of osmotically-active solutes 92
2.4 Measurements of fruit growth and water relations 93
2.4.1 Seasonal variation of fruit growth 93
2.4.2 Diurnal variation of fruit growth 93
2.4.3 Water relations in the fruit flesh and in the stem 93
2.5 Modelling Technique 94
2.6 Description of input data 94
2.7 Initial conditions 95
3 Results 96
3.1 Estimation of model parameters 96
3.2 Test of the model 97
3.3 Analysis of model sensitivity to parameters 98
3.4 Elastic and plastic growth rates 98
3.5 Effect of assimilate or water supply shortage on fruit water relations and composition 99
4 Discussion 100

CHAPITRE V : MODELISATION DE L'ELABORATION DE LA QUALITE DE LA MANGUE 104
1 Introduction 105
2 Matériel et méthodes 107
2.1 Description des modifications apportées aux modèles utilisés 107
2.2 Matériel végétal 110
2.3 Mesures de croissance et de qualité 110

2.4 Description de l'étude virtuelle concernant l'effet de la masse initiale et de la date de récolte sur la croissance et les critères de qualité à la récolte 110
3 Résultats 111
3.1 Test du modèle 111
3.2 Analyse par simulation de l'effet de la masse initiale et de la date de récolte ... 112
4 Discussion 114

CONCLUSIONS ET PERSPECTIVES 118
1 Bilan des connaissances acquises 119
2 Perspectives de recherche 122
2.1 Approfondissement de l'approche écophysiologique 122
2.1.1 Echelle de l'arbre 122
2.1.2 Echelle du fruit 123
2.2 Application de l'approche de modélisation 125

Bibliographie 127

Introduction

Introduction

1 Cadre général

La mangue est un des fruits tropicaux les plus anciens, dont l'origine géographique se situe en Asie du Sud, dans une vaste zone qui s'étend de l'Inde aux Philipines. Elle a été introduite dans de nombreuses régions tropicales et sub-tropicales grâce aux échanges internationaux de marchandises et aux navigateurs. La sélection de ce fruit pour améliorer sa qualité a débuté il y a environ 4000 ans (Laroussilhe de, 1980). Il existerait environ un millier de variétés cultivées à travers le monde (Morton, 1987). Ainsi, dans de nombreuses régions tropicales et subtropicales, la mangue est un des fruits les plus populaires. La mangue est appréciée gustativement et peut être un apport calorique non négligeable pour certaines populations car elle contient des sucres (10 à 15 % de glucides dans la mangue mûre), elle est riche en vitamines (vitamine A et C), minéraux (calcium et potassium) et anti-oxydants (beta-carotène). Elle est également utilisée en médecine pour ses propriétés diurétiques et diététiques.

Actuellement, la production mondiale est d'environ 25-30 millions de tonnes (1999-2000, FAOSTAT 2000), dont 50% provient de l'Inde, 9% de Chine, et 6% du Mexique. Les prédictions pour les années à venir sont une augmentation de la production de 50% pour 2005. La demande en mangues est de plus en plus importante, en particulier durant ces dernières années, de la part des consommateurs des régions tempérées, donc des zones non traditionnelles de production. Le marché européen de la mangue est passé pour ces dix dernières années de 44 000 tonnes (1993) à 120 000 tonnes (2000) de mangue importées, le Brésil et le Mexique étant les principaux fournisseurs de ce marché pendant toute l'année.

Le manguier a été introduit sur l'Ile de La Réunion depuis l'Inde vers 1770. Il est à La Réunion une espèce fruitière majeure, qu'on retrouve dans de nombreuses cours créoles. Le manguier est cultivé sur la façade Ouest de l'île qui a des particularités climatiques et pédologiques favorables à sa culture. La surface cultivée du manguier (16 % de la surface des vergers) a été multipliée par huit en 20 ans, ce qui la situe en troisième position derrière celle du letchi et des agrumes. Cette culture de diversification connaît ces dernières années un essor important, en particulier pour les variétés 'José' (locale) et 'Lirfa' (floridienne) dont environ quatre à cinq mille tonnes sont produites par an. Cet essor se concrétise sur le marché local pour les deux variétés, mais également sur de nouveaux marchés (grande distribution et exportation) plus rémunérateurs, en particulier pour la variété 'Lirfa' qui répond mieux aux critères "export" (fermeté, forme et calibre adaptés, couleur attractive, goût). Les nouveaux marchés sont toutefois plus exigeants en termes de qualité (calibre, goût, maturité, couleur), d'homogénéité des produits, et de régularité de la production.

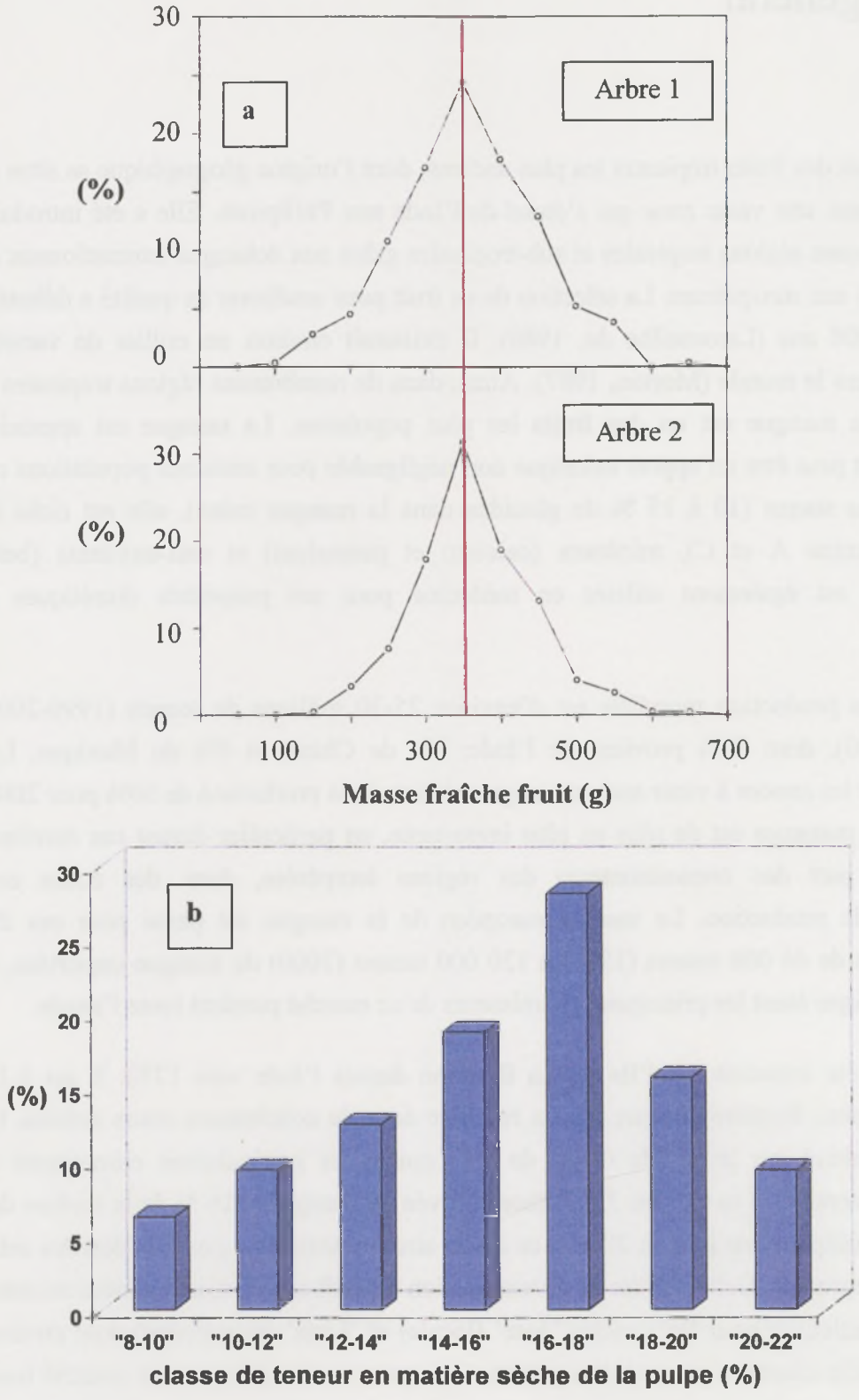

Figure 1 : Distribution à la récolte (a) des masses fraîches de mangues pour deux arbres et (b) de la teneur en matière sèche de la pulpe au sein d'un ensemble de 10 arbres.

1.1 La maîtrise de la qualité, un enjeu pour la mangue

La notion de qualité d'un fruit varie suivant que l'on s'adresse au producteur, au distributeur ou au consommateur. Pour le producteur, la qualité est principalement synonyme de calibre, de précocité, et de résistance aux maladies. Le distributeur caractérise la qualité du produit par sa durée de vie, l'homogénéité des lots de fruits et leur bonne tenue en conservation et durant les transports. Enfin, pour le consommateur, la qualité est plutôt liée à l'aspect extérieur, au goût et à la valeur nutritionnelle du fruit. Depuis plusieurs années, les professionnels des filières fruitières confèrent à la qualité un statut privilégié. Ils sont intéressés par une caractérisation plus complète de cette qualité, qui ne se limiterait pas aux critères dits d'attractivité, comme le calibre et la coloration, mais à des critères liés à la qualité organoleptique du fruit. Cette démarche fait suite à une attention plus particulière que les consommateurs portent sur la spécificité gustative des fruits et sa non standardisation.

Ces considérations générales sur la volonté de mieux maîtriser la qualité des fruits s'appliquent à la culture du manguier dont la demande en produits de qualité est en pleine expansion aussi bien sur les marchés du Nord que du Sud. Pour répondre à ces enjeux, il est nécessaire de mieux comprendre les mécanismes qui interviennent dans l'élaboration de la qualité des fruits, et leurs possibles interactions.

1.2 Le contexte agronomique

La culture du manguier est limitée par (i) une faible productivité, due à une floraison alternante (Singh, 1960), à des variations fortes du nombre d'inflorescences et à une fructification fréquemment très inférieure à la floraison (Chaikiattiyos *et al.*, 1994), et (ii) une hétérogénéité des fruits produits (Jannoyer and Lauri, 2002a; Jannoyer and Lauri, 2002b), conduisant à une mauvaise valorisation de la production. Il en résulte alors une variabilité importante de la production et de la qualité organoleptique des fruits au sein d'une même parcelle et d'un même arbre. On observe notamment une forte hétérogénéité de critères de qualité simples à mesurer, comme le calibre (Figure 1a) et la teneur en matière sèche (Figure 1b) des fruits. Cette variabilité intra-arbre de la qualité des fruits oblige le producteur à réaliser un tri sévère des fruits récoltés avant leur commercialisation car la mise sur le marché des fruits implique l'utilisation de produits homogènes et de qualité. L'analyse de cette variabilité est une étape préalable à la recherche de solutions techniques pour la maîtriser.

1.3 Le projet manguier à La Réunion

Dans ce contexte général et pour répondre à une demande de plus en plus insistante fois des producteurs des pays du sud sur les techniques et les modes de gestion intégrés, productifs et durables en arboriculture fruitière tropicale, une équipe de recherche a été constituée en 2000 et a bénéficié d'une ATP (Action Thématique Programmée du CIRAD) avec pour objectif la maîtrise de la production et de l'élaboration de la qualité organoleptique des fruits chez le manguier. L'influence déterminante de l'alimentation carbonée est l'hypothèse principale retenue pour le fonctionnement du manguier et sa production. Une approche couplant la mise en place d'expérimentations sur les processus qui participent à la mise en production et à l'élaboration de la qualité organoleptique, et l'utilisation des outils de modélisation du fonctionnement de ces processus a été choisie. L'équipe s'organise autour de trois thématiques principales complémentaires : l'organisation architecturale et la structure de l'arbre, l'environnement lumineux et l'acquisition de carbone par la couronne, et la gestion du carbone et de l'eau à différentes échelles (fruit, rameau, arbre) qui ont été associés pour mieux rendre compte de la variabilité spatio-temporelle conditionnant de façon importante la floraison, la production et la qualité organoleptique des fruits et afin de proposer des techniques permettant de mieux maîtriser cette variabilité.

Mon travail de thèse concerne l'étude des processus qui participent à l'élaboration de la qualité organoleptique de la mangue et des facteurs responsables de la variabilité de la qualité dans la plante, dans le but de maîtriser la qualité du fruit au champ. Ces travaux ont été menés au sein de l'équipe du Pôle Fruits, Maraîchages et Plantes Aromatiques (CIRAD-Flhor) située à Saint Pierre (île de La Réunion), en collaboration avec l'unité PSH (Plantes et Systèmes de culture Horticoles) à l'INRA Avignon.

1.4 Objectifs et démarche de l'étude

Le travail de thèse a porté sur l'étude des processus physiologiques qui participent à l'élaboration de la qualité organoleptique de la mangue, sous l'influence de facteurs agronomiques et environnementaux. La démarche développée vise à intégrer les connaissances acquises expérimentalement sur les processus physiologiques dans des modèles. Un objectif important est de prendre en compte les possibles interactions entre les critères de qualité, et d'analyser les causes de variabilité de la qualité des fruits sur un même arbre. L'échelle de travail choisie est le rameau fructifère qui porte les fruits et les feuilles assimilatrices. Ce choix repose sur le fait que le rameau fructifère est (i) l'unité de production et de gestion des arboriculteurs, (ii) une unité relativement autonome dans la plante (Sprugel *et al.*, 1991).

Notre approche doit nous permettre d'analyser dans des conditions contrastées d'alimentation en eau et en carbone :

- le fonctionnement hydrique et carboné de la mangue qui permet sa croissance,
- l'accumulation des sucres, acides et minéraux qui participent à l'élaboration de la qualité organoleptique de la mangue,

et d'intégrer ces résultats dans un modèle de prédiction des caractéristiques du fruit à la récolte (masse fraîche, qualité gustative, indicateurs de la durée de conservation).

2 Facteurs influençant la croissance et l'élaboration de la qualité

La variabilité de la qualité des fruits semble fortement liée à celle de leur croissance. La croissance détermine directement un critère de qualité comme le calibre et la qualité gustative du fruit dépend du niveau de croissance. Ainsi chez la pêche, les fruits ayant une croissance plus longue et plus importante sont les plus sucrés et les moins acides (Génard *et al.*, 1991).

Un fruit est composé en majorité d'eau et de sucres, qui représentent respectivement environ 85 % et 12 % de sa masse fraîche à maturité. L'azote est un composé qui n'est pas très abondant dans le fruit (en moyenne 0.1 % de la masse fraîche d'une mangue). La nutrition azotée influe sur la croissance du fruit en agissant sur l'alimentation carbonée de ce dernier (Habib *et al.*, 1996). Toutefois, l'azote ne semble pas être l'élément qui influence en priorité la croissance et la qualité des fruits. Par contre, les résultats de recherches concernant l'action du carbone et de l'eau sur la croissance et la qualité des fruits de nombreuses espèces soulignent l'importance de ces deux éléments (Miller *et al.*, 1998; Mills *et al.*, 1996; Simmons *et al.*, 1998; Souty *et al.*, 1999).

2.1 Facteurs affectant la croissance du fruit

2.1.1 Alimentation carbonée

Souty *et al.* (1999) montrent que la croissance de pêches augmente avec le nombre de feuilles par fruit. Chacko *et al.* (1982) obtiennent les mêmes résultats sur différentes variétés de mangues (Dashehari, Langra et Totapuri). L'hypothèse de ces relations est la disponibilité en assimilats carbonés qui est liée à la surface de feuilles par fruit et à la photosynthèse des feuilles. Des travaux ont montré un effet positif de la charge en fruits sur la photosynthèse foliaire chez de nombreuses espèces fruitières, comme la pomme (Palmer, 1992), le raisin (Naor *et al.*, 1997), la pêche (Ben Mimoun *et al.*, 1996) et la mangue (Urban *et al.*, 2002). Cet effet est attribué à la régulation de la photosynthèse par la force de puits, associée à l'accumulation des assimilats carbonés dans la feuille (Foyer, 1988). Dans des conditions de disponibilité carbonée limitante, Chacko *et al.* (1982) ont noté une diminution des réserves dans les feuilles. Ceci indique une utilisation rapide des produits de la photosynthèse et une mobilisation des réserves précédemment accumulées pour permettre la croissance des fruits se développant dans ces conditions (Reddy and Singh, 1991).

La croissance résulte pour l'essentiel des importations d'eau et de carbone par les flux xylémien et phloémien et des pertes d'eau par transpiration (Ho *et al.*, 1987; Lee, 1990). Pour tenter d'expliquer les variations de croissance chez la tomate, Guichard (1999) a caractérisé les effets d'une variation de la charge en fruits (nombre de fruits par bouquets) sur les différents flux entrant et sortant du fruit. Cet auteur souligne qu'une modification de l'équilibre source/puits a des effets significatifs sur ces différents flux. Ainsi, de faibles charges en fruits augmentent surtout les flux entrant dans le fruit et dans une moindre mesure les flux sortants. Les fruits reçoivent alors plus d'eau et de carbone et ont une croissance plus rapide.

Les flux d'eau et de carbone sont contrôlés par des gradients de potentiel hydrique et de concentrations. La pression osmotique du fruit est particulièrement sensible à la variation de la concentrations des sucres qui ont un pouvoir osmotique fort, comme les hexoses (Mitchell *et al.*, 1991). Le potentiel hydrique foliaire est lié à la disponibilité de l'eau dans la plante et aux pertes d'eau par transpiration qui sont régulées par la conductance stomatique de la feuille. Les potentiels hydriques des feuilles et des fruits suivent généralement les mêmes tendances (Syversten and Albrigo, 1980). Des auteurs, comme McFadyen *et al.* (1996), ont noté que le potentiel hydrique des feuilles, celui du fruit et la pression osmotique du fruit diminuaient dans les conditions d'une forte charge en fruits. La pression de turgescence des fruits est alors réduite. Dans ces conditions, une réduction de la taille des fruits a été également observée. Ainsi, pour ces auteurs, la variation de la charge en fruits des arbres modifierait le fonctionnement hydrique des fruits, ce qui aurait un impact direct sur leur croissance.

2.1.2 Alimentation hydrique

Des études sur les arbres fruitiers soulignent l'effet du stress hydrique sur la croissance des fruits qui se traduit principalement par une réduction de leur taille, de leur poids frais et une augmentation des teneurs en solutés (Berman and Dejong, 1996; Mills *et al.*, 1996). Un stress hydrique induit des modifications des relations hydriques chez la pomme (Mills *et al.*, 1997) et les agrumes (Huang *et al.*, 2000; Yakushiji *et al.*, 1998) qui se traduisent par une diminution de leur potentiel hydrique, et de leur potentiel osmotique. Les auteurs suggèrent que lors d'un stress hydrique, la pomme est capable d'ajuster son potentiel osmotique et de maintenir sa turgescence. La contribution des acides organiques et l'accroissement de la concentration en sucres dans le fruit pourraient permettre d'expliquer l'ajustement osmotique du fruit (Mpelasoka *et al.*, 2001; Yakushiji *et al.*, 1998).

D'autres auteurs confirment ces observations sur pêcher et poursuivent plus particulièrement la réflexion sur la mise en place d'un stockage plus important des sucres dans les fruits placés en conditions de déficit hydrique. Ils suggèrent que l'acide abscissique, induit lors d'un stress

hydrique, intervient dans l'accroissement du processus d'accumulation des sucres (Kobayashi and Us Salam, 2000). D'après Peel (1965), les facteurs qui affectent le potentiel hydrique xylémien ont un effet direct sur la translocation du phloème. La croissance du fruit étant pour de nombreuses espèces majoritairement déterminée par le flux phloémien (Erhet and Ho, 1986; Grange and Andrews, 1994), des modifications du potentiel hydrique dans la tige influenceraient fortement la croissance du fruit.

Les effets de la transpiration sur la croissance du fruit a été étudiée. Lescourret *et al.* (2001) ont simulé la croissance en matière fraîche et l'état hydrique de la pêche au cours d'une saison. Un des résultats est que plus la perméabilité cuticulaire à l'eau est faible, plus la masse fraîche du fruit est importante. Ils remarquent également avec les simulations que l'augmentation de la perméabilité au cours du développement du fruit pourrait être responsable de l'arrêt de la croissance du fruit. Li *et al.* (2001) ont modifié l'environnement proche des fruits en les recouvrant d'un film plastique. La transpiration du fruit et sa croissance en masse sèche s'en trouvent réduites. Ainsi, la modification d'un des flux intervenant au niveau du fruit semble induire des variations des autres flux, ce qui n'est pas sans conséquence pour la croissance et la qualité du fruit.

2.2 Elaboration de la qualité

2.2.1 Alimentation carbonée

Les flux d'assimilats influencent fortement la composition et donc la qualité des fruits (Souty *et al.*, 1999; Volz *et al.*, 1993). Chez la pêche, l'accumulation du saccharose augmente avec le nombre de feuilles par fruit. Des indicateurs de la qualité gustative comme le rapport entre les concentrations en acide malique et acide citrique, et l'acidité titrable présentent des allures bien différentes selon la charge en fruits (Poll *et al.*, 1996; Wu *et al.*, 2002). Les fruits qui se sont développés dans des conditions de faible rapport feuilles/fruit sont plus acides au goût à maturité. La chair de ces fruits contient en fait des teneurs en saccharose plus faibles et en acide citrique plus importantes, ce qui modifie le rapport sucres/acides (Souty *et al.*, 1999).

Simmons *et al.* (1998) ont complété ce type d'étude chez une variété de mangue, Kensington Pride, en caractérisant les effets de rapports feuilles / fruit variables sur la concentration en éléments minéraux et certains critères de qualité (coloration, fermeté, sucres solubles totaux et acidité de la pulpe). Ces auteurs s'intéressent plus particulièrement au calcium. Le calcium est en effet associé à la qualité du fruit par son rôle sur le mûrissement et la sénescence (Ferguson, 1984). Il retarderait la mise en place de ces deux processus et réduirait les désordres physiologiques au cours de la conservation des fruits (Bangerth, 1979). Les résultats de leurs travaux montrent qu'un équilibre optimal entre la taille, la qualité du fruit et la teneur en calcium est atteint pour un rameau comportant 60 feuilles par fruit.

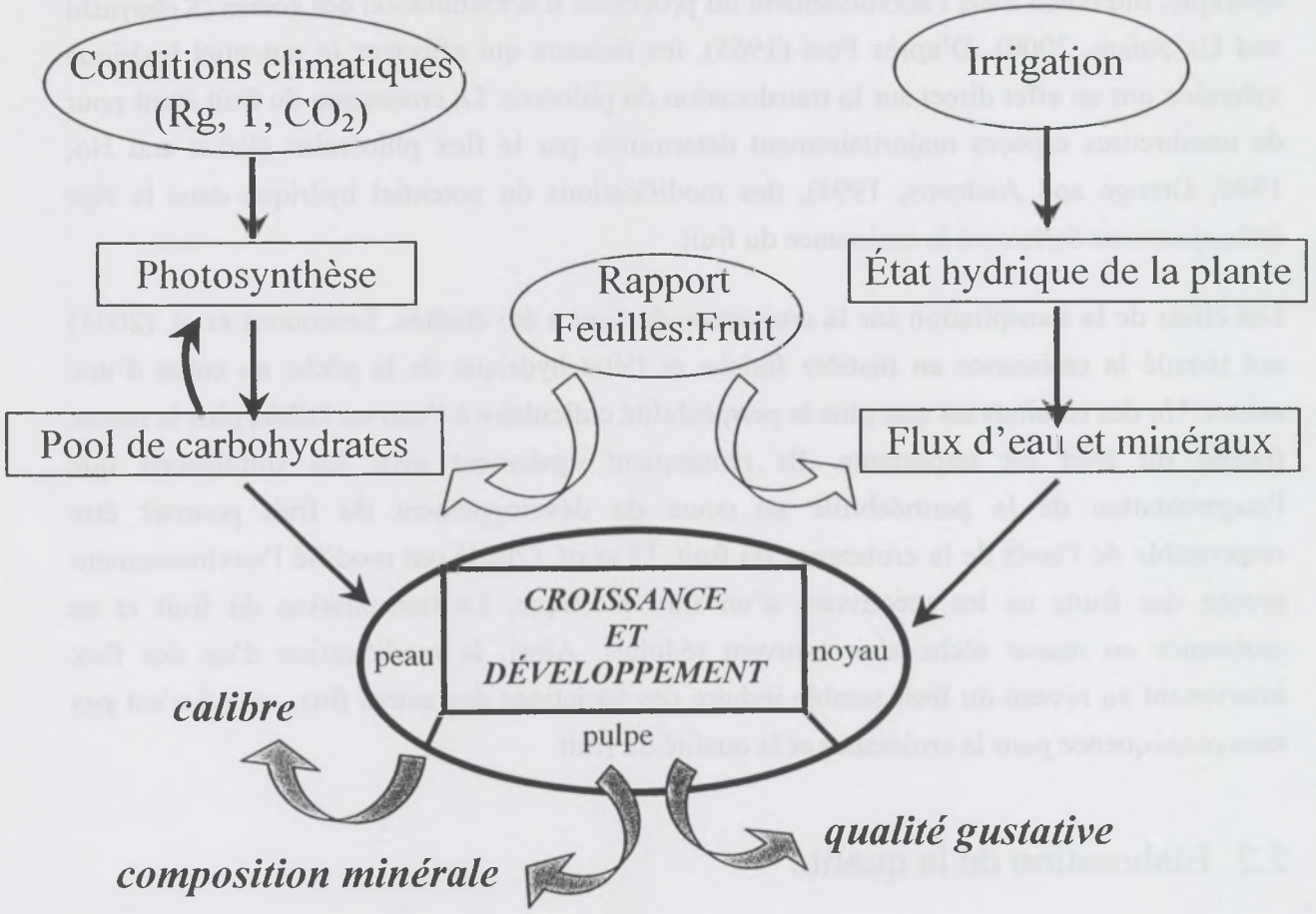

Figure 2 : Hypothèses de travail pour analyser l'élaboration de la qualité de la mangue et les facteurs qui l'affecte.

Les résultats de Poll *et al.* (1996) suggèrent qu'une meilleure disponibilité de la fourniture en assimilats, due en particulier à un rapport feuilles/fruit élevé, entraîne une augmentation de l'accumulation des précurseurs des acides gras aromatiques et des arômes dans la pomme. La voie métabolique du shikimate est importante car elle relie le métabolisme de composés secondaires, comme certaines vitamines, au métabolisme des sucres (Jensen, 1985). Ainsi, des variations de la disponibilité en assimilats carbonés peuvent modifier le métabolisme de ces composés secondaires qui participent à l'élaboration de la qualité nutritionnelle du fruit.

2.2.2 Alimentation hydrique

Un déficit hydrique appliqué au cours de la saison a des conséquences sur la qualité du fruit. Un accroissement des concentrations en sucres est généralement observé au moment où le déficit hydrique commence à être marqué, chez la pomme (Kilili *et al.*, 1996), la mandarine (Yakushiji *et al.*, 1998) et la baie de raisin (Esteban *et al.*, 1999). L'acidité du fruit, et plus particulièrement les teneurs en acides citrique et malique peuvent être affectées par des variations de l'alimentation hydrique (Gonzàlez-Altozano and Castel, 1999; Wu *et al.*, 2002). Cet effet de l'alimentation hydrique peut être dû à une réduction du transport des acides vers le fruit (Andersen *et al.*, 1995) ou à une dilution des acides dans le fruit (Mpelasoka *et al.*, 2000). Les concentrations en éléments minéraux, comme le calcium sont plus faibles dans les fruits exposés à un stress hydrique (Behboudian *et al.*, 1994; Mills *et al.*, 1994). La fermeté du fruit et la pigmentation de la peau varient également avec l'alimentation hydrique (Mills *et al.*, 1994). L'apparition plus rapide de la couleur rouge de la peau est due aux anthocyanes dont la synthèse nécessite du saccharose, sucre s'accumulant plus rapidement dans les fruits d'arbres non irrigués, et à la réduction de la teneur en azote qui est un constituant des pigments chlorophylliens. L'application d'un stress hydrique semble avoir tendance à améliorer certains critères de qualité et à accélérer la maturité des fruits.

Ces différentes expérimentations montrent que l'alimentation carbonée influence la croissance par ses effets sur les relations sources/puits. Au niveau des sources, la photosynthèse et la mise en réserves ou leur mobilisation peuvent être affectées (Figure 2). Au niveau des puits, la disponibilité des assimilats carbonés joue sur les flux de carbone, mais aussi fortement sur les flux d'eau entrant et sortant du fruit et par conséquent sur l'état hydrique du fruit (Figure 2). L'alimentation carbonée et hydrique affecte l'élaboration de la qualité organoleptique du fruit principalement par leurs effets sur la composition du fruit en sucres, acides organiques et éléments minéraux (Figure 2). Dans mon travail de thèse, je me suis tout d'abord intéressé à vérifier ces hypothèses (Figure 2) généralement établies pour des fruits tempérés, sur un fruit tropical, la mangue, en considérant les différents compartiments du fruit (peau, pulpe, noyau). Ce fruit possède en outre un noyau plus volumineux que ce qui est habituellement rencontré

chez les fruits consommés. Il était donc important d'en étudier les coûts de construction. Nous avons analysé le couplage de l'accumulation de l'eau et du carbone dans les différents compartiments du fruit, puis les conséquences de ce couplage sur l'élaboration de la qualité dues aux effets sur la teneur en matière sèche, sur la proportion de parois, et sur la teneur des principaux composés. Ensuite, l'analyse des processus impliqués dans la croissance et l'élaboration de la qualité et affectés par la disponibilité hydrique et carboné est réalisée par une approche intégrée de manière à prendre en compte les interactions entre les processus. Pour cette intégration, nous avons utilisé l'outil de modélisation.

3 La modélisation : outil d'étude du fonctionnement du fruit

La modélisation peut être un outil puissant pour analyser les processus physiologiques et leurs interactions. Dans le cadre du système complexe qu'est le rameau fructifère, le modèle doit prendre en compte les principaux processus impliqués dans le fonctionnement carboné du rameau et du fruit (photosynthèse, dynamique des réserves, allocation des assimilats, composition et croissance du fruit) et dans leur fonctionnement hydrique (flux d'eau entrant et sortant, et état hydrique du rameau et du fruit).

La croissance des fruits a été modélisée à de nombreuses reprises par différentes approches. Certains auteurs ont utilisé une approche stochastique de la vitesse de croissance (Hall *et al.*, 1996). Toutefois, la partie végétative de la plante n'est pas prise en compte ce qui limite l'étude de l'effet des conditions climatiques et des pratiques culturales sur la croissance du fruit. De plus, l'extrapolation de ces modèles empiriques à d'autres espèces ou d'autres environnements (localisation, climat) peut parfois poser des problèmes. Une autre approche, basée sur la description de l'assimilation et de l'allocation du carbone, qui inclut l'effet des conditions climatiques, a été proposée sur kiwi (Buwalda, 1991) et pêche (Grossman and Dejong, 1994). Ces modèles qui regroupent les organes de la plante en compartiment (fruits, feuilles, tiges et racines), ne permettent pas la prise en compte de la variabilité au sein d'un même arbre. Pour pallier cette limitation, la modélisation du fonctionnement carboné d'un rameau fructifère a été proposée sur pêcher (Lescourret *et al.*, 1998). Ce modèle permet de rendre compte de la variabilité de la croissance en matière sèche du fruit selon les conditions d'environnement lumineux et d'alimentation carbonée du rameau (Génard *et al.*, 1998).

Les flux d'eau entrant dans le fruit et les flux de transpiration ont été représentés soit par une approche empirique (Génard and Huguet, 1996; Lee, 1990), soit par une approche mécaniste de type biophysique (Fishman and Génard, 1998). Cette dernière approche représente les échanges d'eau et de matière sèche entre la plante et le fruit en considérant les flux phloèmiens et xylémiens, et entre le fruit et son environnement en tenant compte des pertes de carbone et d'eau par respiration et transpiration. La croissance irréversible et l'état hydrique du fruit sont modélisés en appliquant la théorie de la croissance cellulaire pilotée par la pression de turgescence, proposée par Lockhart (1965).

L'élaboration de la qualité a été peu modélisée. Des modèles mécanistes d'accumulation des sucres (Génard and Souty, 1996) et des acides (Lobit *et al.*, 2003) chez la pêche ont été proposés.

La modélisation peut permettre d'analyser les effets de pratiques culturales, liées à l'irrigation ou à la charge en fruit, sur la croissance (Doyle *et al.*, 1989; Fishman and Génard, 1998; Génard and Huguet, 1996; Lescourret *et al.*, 1998) et sur la qualité des fruits (Génard *et al.*, 2003).

Les bases de certains de ces modèles (Fishman and Génard, 1998; Lescourret *et al.*, 1998) ont été reprises dans le cadre de cette thèse pour développer un modèle de fonctionnement carboné et hydrique pour le rameau de manguier. Le modèle construit au cours de la thèse a été utilisé dans des études virtuelles. Ces dernières permettent de bien contrôler des facteurs internes à la plante et de faire varier chaque facteur un par un pour une étude complète des effets du climat, de facteurs internes à la plante et de facteurs affectant les relations sources/puits (alimentation carbonée et hydrique) sur les processus physiologiques impliqués dans la croissance et l'élaboration de la qualité de la mangue. Cette approche intégrative est nécessaire pour envisager le pilotage des pratiques culturales, comme l'irrigation et celles influençant l'alimentation carbonée, par des simulateurs ayant pour objectif la maîtrise de la qualité organoleptique.

4 Plan du travail

Dans une première partie, le fonctionnement carboné et hydrique de la mangue est présenté à travers une étude descriptive. Une première étude porte sur l'effet de la disponibilité carbonée (en faisant varier le rapport feuilles/fruit) sur l'accumulation de la matière sèche mais également de l'eau dans les différents compartiments du fruit (peau, pulpe, et noyau). Cette partie permet de proposer des relations empiriques entre la masse d'eau et la masse sèche de chaque compartiment et de formaliser de manière descriptive le lien entre l'alimentation carbonée et l'eau dans la mangue. Une deuxième étude descriptive porte sur l'effet de l'alimentation carbonée et hydrique (en faisant varier le rapport feuilles/fruit et l'irrigation) sur la composition biochimique de la mangue en croissance. Cette étude nous a permis de préciser si ces facteurs influencent l'élaboration de la qualité chez la mangue, et quels sont les critères de qualité les plus affectés (teneur en matière sèche, sucres, acides organiques, éléments minéraux).

Dans une deuxième partie, l'étude du fonctionnement carboné de la mangue au niveau du rameau fructifère est abordée. L'assimilation de carbone, sa régulation par la demande des puits, et la dynamique des réserves, ont été caractérisées au niveau des sources. Au niveau des puits, l'allocation de carbone, les coûts de constructions des principaux compartiments (la peau, la pulpe et le noyau) et la croissance en masse sèche du fruit ont été déterminés. Nous avons analysé l'activité "puits" d'un fruit qui dépend des conditions de sa croissance dans le passé et de la taille initiale du puits. Une étude virtuelle basée sur la modélisation de la croissance en matière sèche du fruit nous a permis de quantifier les effets des conditions climatiques, de pratiques culturales, de facteurs internes à la plante et des interactions entre ces facteurs sur les processus physiologiques impliqués dans la croissance du fruit.

Dans une troisième partie, nous présentons l'étude du fonctionnement hydrique de la mangue. Des expérimentations ont été mises en place sur la croissance en volume du fruit, l'état hydrique du rameau et du fruit pour analyser les propriétés plastique et élastique de la mangue. Ces expérimentations nous ont permis de proposer des lois de variation des paramètres liés à la plasticité et à l'élasticité des tissus et de construire un modèle du fonctionnement hydrique du fruit capable de rendre compte de la croissance plastique et élastique de la mangue. Les résultats de l'expérimentation sur l'élaboration de la qualité du fruit ont été introduits dans ce modèle pour construire un modèle empirique de la composition biochimique de la pulpe qui permet d'en calculer le potentiel osmotique. Ce modèle de fonctionnement hydrique du fruit est également utilisé pour simuler l'autre composante de l'état hydrique du fruit, la pression de turgescence. La modélisation du fonctionnement

hydrique de la mangue a permis au cours d'une étude virtuelle d'analyser l'effet d'une réduction de la disponibilité carbonée et hydrique sur la croissance, les relations hydriques et la composition biochimique du fruit.

Dans une quatrième partie, nous présentons l'intégration des deux modèles sur le fonctionnement carboné et hydrique du fruit dans un modèle global au niveau du rameau fructifère. Ce modèle global est utilisé pour simuler la croissance en matière fraîche de la mangue. Il prédit différents critères de qualité à la récolte, comme le masse fraîche, les concentrations en sucres, acides et éléments minéraux, et l'évolution de la saveur sucrée et acide du fruit.

Chapitre I : Matériels et méthodes

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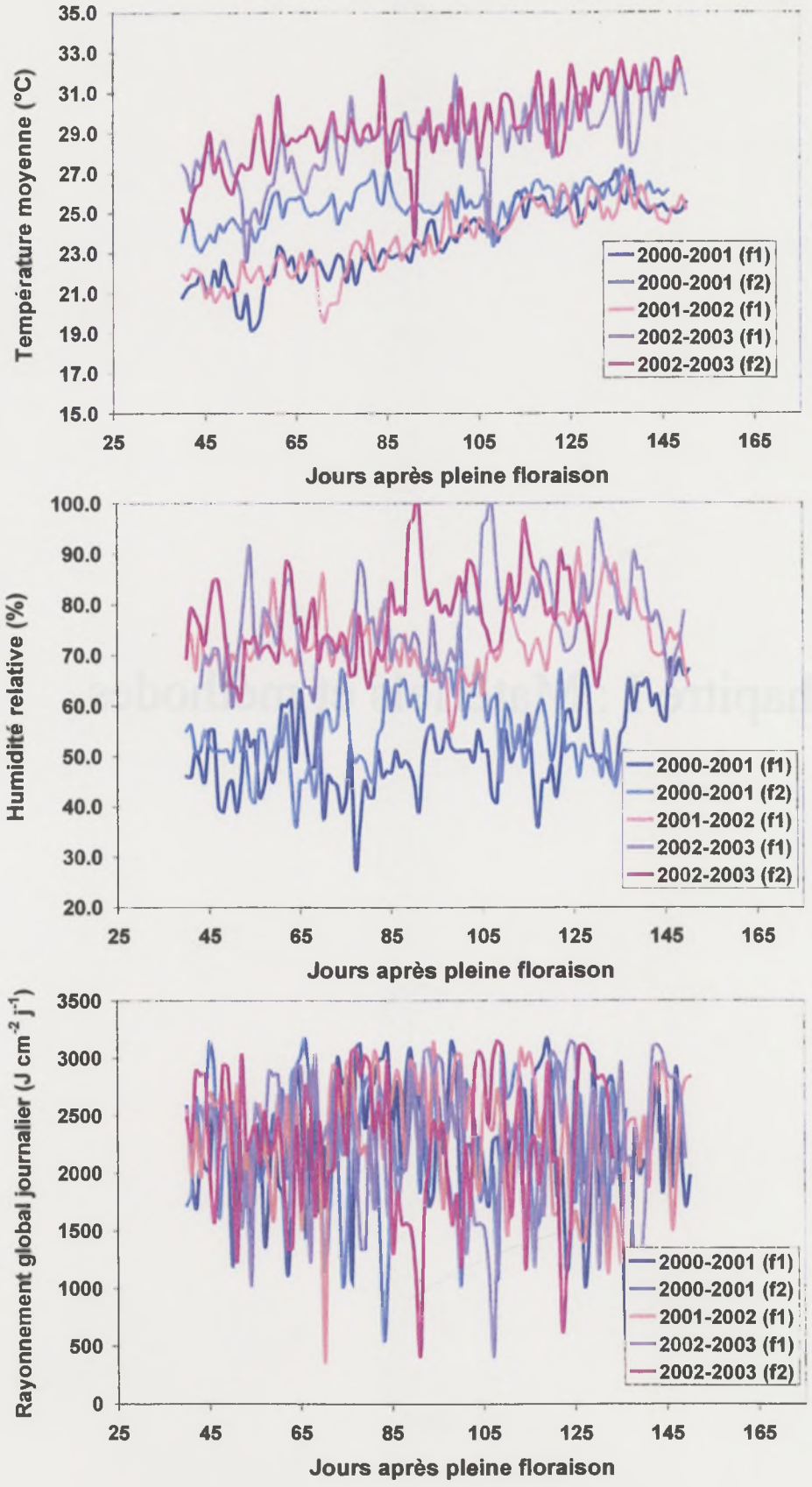

Figure 1 : Données climatiques journalières : température moyenne (a), humidité relative moyenne (b) et rayonnement global cumulé (c) au cours des première ("f1") et deuxième ("f2") floraisons des trois années d'expérimentations.

1 Conditions et dispositifs expérimentaux

1.1 Conditions expérimentales

1.1.1 Le site expérimental de la station du CIRAD-FLHOR à Bassin Plat

Le verger d'expérimentation se trouve sur la station CIRAD de Bassin Plat, à Saint Pierre (Ile de la Réunion, 20°52'48''S, 55°31'48''E), à une altitude d'environ 150 m. Ce verger de manguiers (Mangifera indicae) du cultivar "Lirfa" est constitué d'arbres agés de 11 ans (en 2000), greffés sur le porte-greffe "Maison Rouge", caractérisé par un enracinement puissant favorisant une bonne résistance aux vents cycloniques et à la sécheresse. Le cultivar "Lirfa" offre des avantages très intéressants pour les arboriculteurs : c'est un cultivar précoce dont la récolte est groupée entre le 15 décembre et le 15 février, pouvant ainsi éviter des pertes de production causées durant la période cyclonique de fin janvier à mi-mars et minimisant égalemenent les impacts de la bactériose (Xanthomonas campestris pv. Mangiferaeindicae). Le verger est séparé en deux par une haie d'acacia brise-vent. La parcelle 1 de ce verger est composée de 10 rangées comprenant chacune 8 à 9 manguiers, dont l'espacement est de 4 m entre les arbres de la même rangée, et de 6 m entre les arbres de deux rangées voisines. La parcelle 2 de ce verger est composée de 8 rangées dont l'espacement entre les arbres est de 5 m sur une même rangée, et de 6 m entre les rangées. Les arbres ont atteint une hauteur d'environ 3 m. La parcelle 1 a été utilisée pour les expérimentations en 2000 et 2002, alors que la parcelle 2 a accueilli les expérimentations en 2001 et 2002.

1.1.2 Suivi des paramètres climatiques

1.1.2.1 Données météorologiques de la station du CIRAD

Les données climatiques journalières (température moyenne, rayonnement global cumulé, et humidité relative moyenne) enregistrées sur la station météorologique du CIRAD située sur le site de Ligne Paradis (Saint Pierre), au cours des trois années d'expérimentation sont présentées en Figure 1. La saison de croissance 2002-2003 se caractérise par des températures et des humidités relatives plus élevées. Les températures les plus fraîches ont eu lieu au cours de la saison de croissance 2000-2001 issue de la première floraison et de la saison 2001-2002. La saison 2000-2001 se caractérise par une atmosphère plus sèche, quelque soit l'origine des fruits (première ou deuxième floraison). Peu de différences entre saisons se dégagent des

Figure 2 : Vue d'un rameau décortiqué (a) sur lequel les mangues (b) sont repérées pour l'étude de leur croissance et de leur qualité.

données de rayonnement global journalier qui semblent être très variable au cours d'une même saison de croissance.

1.1.2.2 Mesure du climat au voisinage du couvert

Une station météorologique a été installée en 2001 dans le verger d'expérimentation. Un capteur de rayonnement (PAR, Photosynthetically Active Radiation) a été placé au dessus du couvert, et des capteurs de température et d'humidité de l'air ont été installés dans le couvert (environ à 2 m).

Les données acquises par la station du CIRAD et par la station sur la parcelle d'expérimentation ont été comparées. Les résultats ont montré que les données météorologiques des deux stations sont comparables. Nous avons choisi d'utiliser les données acquises sur la station météorologique du CIRAD pendant toute mon étude.

Le climat au voisinage du fruit a été caractérisé par des mesures de température moyenne. Des thermocouples (cuivre-constantan) ont été installés à la surface de ces fruits. Les résultats montrent que la différence entre la température de l'air et celle de la surface du fruit n'est pas très importante. En première approximation, la température de l'air a été considérée comme une bonne estimation de celle du fruit.

1.2 Dispositifs expérimentaux

Chaque année, un suivi de la floraison a été effectué de manière à noter les floraisons successives, et la date pour laquelle 50 % des inflorescences étaient ouvertes, qui correspond à la pleine floraison. Cette date est choisie comme le point de départ du développement du fruit.

1.2.1 Modification du rapport feuilles/fruit par décortication

Généralement, six semaines après la floraison, entre 10 et 15 branches par arbre sont repérées, situées le plus souvent dans les parties supérieures du couvert pour réduire la variabilité de l'éclairement reçu par les feuilles qui influence leur activité photosynthétique (comm. pers., L. Urban), et affecte alors l'assimilation nette de carbone et la croissance du fruit. Une annélation est pratiquée à la base du rameau étudié afin de l'isoler du reste de l'arbre du point de vue du fonctionnement carboné. La décortication annulaire consiste à enlever le phloème sur une largeur de 10 à 15 mm à l'aide d'un greffoir (Figure 2a). Le xylème reste intact, les flux hydriques sont donc conservés en grande partie. Selon le traitement "nombre de feuilles par fruit", quelques fruits ou feuilles peuvent être retirés du rameau fructifère. Toutefois un

seul fruit par panicule est conservé pour éviter la compétition entre les fruits au sein de la même panicule (Figure 2b). Durant la croissance du fruit, les pousses végétatives qui apparaissant sur les rameaux sont retirées pour conserver un rapport feuilles/fruit constant. La décortication du rameau a lieu quand la longueur du fruit est d'environ 5 cm. A ce stade de développement, la chute physiologique des fruits qui diminue fortement le nombre de fruits restants par rameaux, est terminée.

1.2.2 Variation de l'irrigation

Nos expérimentations, en 2000 et 2002, ont été conduites dans des conditions d'arrosage non limitantes. Tous les deux jours, une irrigation correspondant à la somme de l'évapotranspiration de ces deux journées était effectuée. En 2001, un traitement "non irrigué" a été appliqué sur une partie des arbres de la parcelle, l'autre partie des arbres étant irriguée de façon non limitante dans les mêmes conditions que les deux autres années. Dans le traitement "non irrigué", l'irrigation a été arrêtée un mois après la pleine floraison. Les arbres ont alors reçu uniquement de l'eau provenant des précipitations, soit environ 170 mm entre la mise en place du traitement "non irrigué" et la fin de la saison de croissance des fruits. La parcelle a été divisée en six blocs de 9 arbres, de manière à ce que les fruits étudiés soient portés par un arbre entouré de huit arbres recevant le même traitement d'irrigation. Le même traitement d'irrigation a été appliqué sur trois blocs différents.

2 Mesures et analyses effectuées

2.1 Caractérisation des organes sources

Partie détaillée dans le Chapitre III Combined effects of climate and source / sink relations on mango fruit growth studied by a modelling approach.

Nous avons mesuré l'activité photosynthétique des feuilles des rameaux décortiqués en 2000, 2001 et 2002 (travail piloté par Laurent Urban). Les mesures effectuées en 2000 et 2001 sur les feuilles des traitements 25, 50 et 100 ont été utilisées pour obtenir la relation entre la photosynthèse à rayonnement saturant et la demande des fruits. Quelque soit le dispositif utilisé, la méthode de mesure de la photosynthèse était la même.

La surface foliaire totale du rameau a été obtenue par une relation allométrique établie avec le nombre de feuilles, à partir de données acquises dans le cadre de l'ATP (Action Thématique Programmée) CIRAD.

Au cours des expérimentations menées en 2000, nous avons récolté les feuilles sur lesquelles les mesures de photosynthèse ont été effectuées et le bois des rameaux correspondants. La biomasse fraîche de chaque compartiment était pesée, puis un échantillon était séché dans une étuve ventilée à 70°C, puis pesé. Un autre échantillon était lyophilisé, puis des analyses de son contenu en sucres solubles et amidon étaient réalisées pour déterminer les réserves de chaque compartiment.

2.2 Caractérisation des organes puits

2.2.1 Etude de la croissance saisonnière des fruits

Partie détaillée dans le Chapitre III Combined effects of climate and source / sink relations on mango fruit growth studied by a modelling approach.

Nous avons étudié la croissance des fruits à partir de deux méthodes : soit par un suivi toutes les semaines des trois dimensions (diamètre, largeur et longueur) du même fruit au cours de la saison ("suivi non destructif") à l'aide d'un pied à coulisse électronique à affichage digital, soit par des pesées de fruits récoltés à des dates successives au cours de la saison ("suivi destructif"). En 2000, les fruits pesés lors du "suivi destructif" ont également été mesurés de

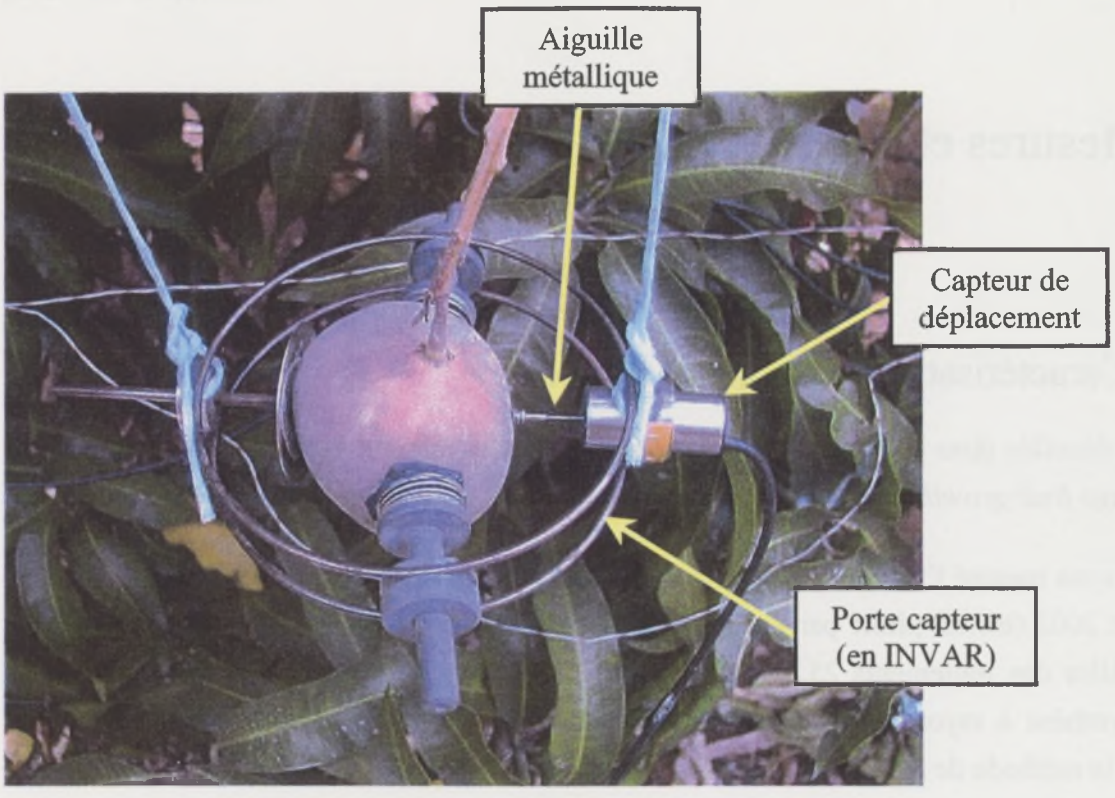

Figure 3 : Vue du dispositif de mesures des variations du diamètre de la mangue. (capteur déplacement, porte capteur en invar, aiguille)

manière à établir des relations allométriques entre le diamètre et le masse fraîche ou sèche des fruits.

2.2.2 Etude de la croissance horaire des fruits

Durant nos expérimentations, la croissance des fruits a également été suivie à partir de capteurs de déplacement (Solartron, type DF 5.0, France) composés d'une bobine de fer doux et d'une tige sensible métallique. La croissance du fruit induit le déplacement de l'aiguille métallique qui perturbe le champ magnétique créée par la bobine du capteur. Le signal émis est alors enregistré automatiquement toutes les 10 secondes par une centrale d'acquisition de données (10X ou 21X, Campbell Scientific Ltd, Shepshed, Angleterre) et moyenné toutes les heures. Le capteur est alimenté par une source de courant continu (environ + 12 V), dont la tension exacte est également enregistrée. Le signal mesuré est converti en mm, à partir des valeurs du signal, de la tension d'alimentation et du coefficient de sensibilité du capteur utilisé. Le capteur est positionné sur le diamètre équatorial de la mangue grâce à des porte-capteurs en INVAR, un alliage dont le coefficient de dilatation est voisin de zéro (Figure 3). Les variations de diamètre enregistrées sont transformées en variations de masse sèche et de masse d'eau à partir de relations allométriques (Chapitre IV).

Partie détaillée dans le Chapitre IV An analysis of elastic and plastic fruit growth in response to various assimilate supplies.

En 2001, nous avons mesuré pendant une journée (le 4 Décembre) les variations horaires du diamètre de deux fruits provenant des traitements 10 et 100 feuilles par fruit. En 2002, nous avons mesuré au cours de trois périodes qui ont duré de cinq à sept jours (entre le 8 Novembre et le 17 Décembre) les variations du diamètre de onze fruits du traitement 100 feuilles/fruit.

2.2.3 Etude de l'état hydrique des fruits

Partie détaillée dans le Chapitre IV An analysis of elastic and plastic fruit growth in response to various assimilate supplies.

En 2001 et 2002, l'état hydrique du fruit et celui du rameau ont été suivis au cours de journées particulières. Pour cela nous avons mesuré le potentiel hydrique de feuilles qui ont été emballées trois heures avant la mesure (Figure 4a) de manière à ce que leur contenu en eau soit en équilibre avec celui du rameau. Le potentiel hydrique foliaire mesuré est considéré égal à celui du rameau. Le potentiel hydrique de la mangue a été mesuré sur des morceaux de pulpe fraîche à l'aide d'un appareil mesurant le point de rosée (WP4, Decagon Devices, Inc. Pullman, Washington, USA) (Figure 4b). La pression osmotique du jus extrait de ces

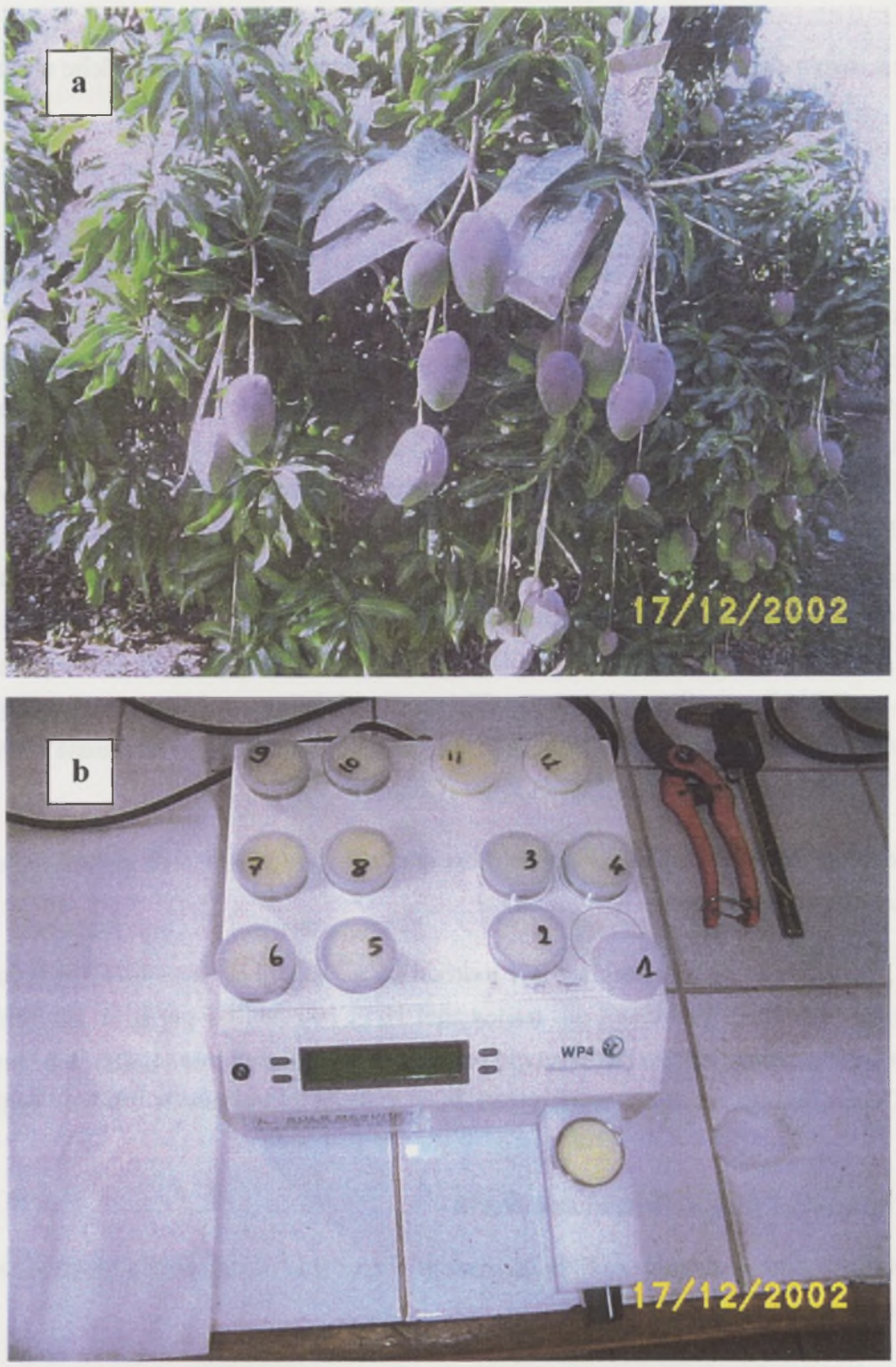

Figure 4 : Feuilles emballées pour des mesures du potentiel hydrique de tige (a) à l'aide de la chambre à pression, et disques de tissus de pulpe de mangue pour des mesures de leur potentiel hydrique (b) à l'aide du WP4.

morceaux de pulpe qui ont été congelés puis broyés a été mesurée à l'aide d'un osmomètre (Wescor, Logan, Utah USA).

2.2.4 Etude de la composition biochimique des fruits

Partie détaillée dans le Chapitre II-2 Leaf to fruit ratio and irrigation supply affect seasonal changes in minerals, organic acids, and sugars of mango fruits.

Chaque année d'expérimentation, une partie de la pulpe des fruits récoltés au cours du "suivi destructif" a été conservée pour des analyses en sucres solubles (glucose, fructose, saccharose), en acides organiques (acides malique, citrique, pyruvique, oxalique) et en éléments minéraux (K^+, Mg^{2+}, Ca^{2+}, NH_4^+, Na^+).

En 2000, des analyses complémentaires consistant à mesurer les teneurs en carbone, azote et cendres des différents compartiments du fruit (peau, pulpe et noyau) ont été effectuées sur les fruits récoltés au cours du "suivi destructif" pour calculer les coûts énergétiques de biosynthèse de chaque compartiment (*Partie détaillée dans le Chapitre III Combined effects of climate and source / sink relations on mango fruit growth studied by a modelling approach).*

2.2.5 Etude du nombre de cellules à la fin de la croissance

Cet essai a été réalisé en 2002 sur 18 fruits mûrs du traitement 100 feuilles/fruit dans le but d'évaluer la taille des puits par comptage du nombre de cellules. Nous avons utilisé une méthode mise au point sur tomate (Bertin *et al.*, 2002). Pour chaque fruit récolté, la peau, la pulpe et le noyau sont séparés délicatement. La totalité de la pulpe est pesée, coupée en morceaux et digérée dans une solution contenant 3.5% de pectinase, 0.1M d'EDTA, 0.4M de mannitol et une pincée d'antioxydant (sodium sulfite). Le pH de la solution de macération est de 4 et la digestion dure 2 à 3 jours à 32°C. Après agitation de la solution, on en prélève un échantillon de quelques µL qu'on dépose sur une lame de comptage (Fuchs-Rosenthal, 0.2 mm de profondeur). Trois prélèvements successifs sont réalisés dans le bas, le milieu et le haut du bécher contenant la pulpe en macération. Le nombre total de cellules contenues dans la pulpe est déduit pour chaque échantillon prélevé du nombre de cellules compté sur la lame de comptage, du volume de cette lame, de celui de la solution de macération et de celui de la pulpe. Le nombre de cellules moyen de la pulpe est ensuite calculé comme la moyenne des 9 répétitions.

3 Analyses statistiques

Partie détaillé pour chaque Chapitre dans le paragraphe "statistical analysis" ou "modelling technique".

Des analyses de variance suivies de test de comparaison de moyenne de Tukey ont été effectuées pour tester l'effet des traitements, sur la croissance et l'élaboration de la qualité du fruit. Les relations allométriques et les paramètres de modèle empirique (potentiel hydrique rameau, composition de la pulpe) ont été obtenus par des régressions linéaires et non linéaires selon les cas. L'estimation des paramètres des modèles est réalisée par une régression non linéaire en minimisant un critère par la méthode des moindres carrés. L'ensemble des procédures statistiques ont été réalisées avec le logiciel SPlus (Insightful Corp., USA).

Chapitre II : Effets de l'alimentation carbonée et hydrique sur l'élaboration de la qualité de la mangue

Chapitre II : Effets de l'alimentation carbonée et hydrique sur l'élaboration de la qualité de la mangue

Le calibre du fruit est un critère de qualité qui dépend fortement de l'accumulation d'eau et de matière sèche dans les trois compartiments du fruit : le noyau, la pulpe et la peau. Il apparaît donc intéressant d'analyser l'accumulation d'eau et de matière sèche dans chaque compartiment, de façon à différencier la pulpe qui est le compartiment du fruit qui intéresse le plus le consommateur du noyau et de la peau. L'étude de l'effet de la disponibilité en assimilats carbonés sur le contenu en eau et en matière sèche des différents compartiments de la mangue au cours de sa croissance est présentée dans une première partie (Léchaudel, M., Génard, G., Lescourret, F., Urban, L. et Jannoyer, M. Leaf-to-fruit ratio affects water and dry matter content in mango fruit. 2002. *Journal of Horticultural Science & Biotechnology*, 77, 773-777).

Dans une seconde partie, les effets de la disponibilité hydrique et carbonée sur l'élaboration du critère de qualité de la mangue défini par la concentration des principaux sucres acides organiques et éléments minéraux (en gramme par gramme de matière fraîche) sont présentés. Dans le but de séparer l'effet de dilution dû aux variations de l'alimentation hydrique ou carbonée, de l'effet plus direct des traitements sur le contenu de chaque composé par unité de paroi, le critère de qualité étudié est décomposé en trois composantes : la teneur en matière sèche totale de la pulpe, la teneur en matière sèche structurale, et la concentration de chaque élément par gramme de matière sèche structurale. L'effet de ces facteurs agronomiques sur chaque composante est alors quantifié (Léchaudel, M., Joas, J., Caro, Y. M., Génard, M. and Jannoyer, M. Leaf to fruit ratio and irrigation supply affect seasonal changes in minerals, organic acids, and sugars of mango fruits. Manuscript soumis à *Journal of the Science of Food and Agriculture*).

1 Leaf-to-fruit ratio affects water and dry matter content in mango fruit.

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SUMMARY

Changes in water and dry matter content of developing mango fruit (*Mangifera Indica* L. cv. 'Lirfa') were investigated over a single season in Réunion Island, along with the effects of leaf:fruit ratio (10, 25, 50, 100 and 150 leaves per fruit on girdled branches). As the fruit developed, about 8-13% of fruit water weight was in the peel compared with 78-86% in the pulp and 6-9% in the stone. When the data were expressed on a dry weight basis, 12-20% was in the peel, 60-70% was in the pulp and 18-20% in the stone. At harvest, larger fruit, on treatment 100, had a higher proportion of weight in the pulp. Good relationships between water and dry weight of each fruit component were found, regardless of the treatment. They showed that the rate of water accumulation decreased when the dry weight increased and that the dry matter content increased as the fruit developed as well. Increasing leaf:fruit ratio to 100 leaves per fruit improved fruit yield by 300 g and pulp dry matter content by 6%, for a total of 550 g and 20% at harvest. Fruit quality as estimated by pulp dry matter content could be easily calculated during the changes in fruit weight over the season. Moreover, this indicator could be useful to assess the maturity of mango fruit.

1.1 Introduction

Fruit growth involves the net accumulation of water and dry matter in the reproductive tissues. Fleshy fruit such as tomato and mango are more than 80% water (Ho *et al.*, 1987; Lakshimnarayana *et al.*, 1970)

The dry matter content of fruit, especially of the pulp, is important from the point of view of quality since it is linked to various quality traits such as total soluble solids in kiwifruit (Richardson *et al.*, 1997) and mango (Diczbalis *et al.*, 1995). (Hofman *et al.*, 1995) found that mango fruits with higher dry matter content ripened more quickly and had a better gustatory quality. Moreover, Diczbalis *et al.* (1995) suggested that dry matter content could be useful to assess fruit maturity.

Dry matter content is strongly linked to water and dry matter accumulation (Ho *et al.*, 1987). Water is supplied by the phloem as well as the xylem. Water loss is often equivalent to water imported by xylem (Huguet and Génard, 1995) for fruits with low transpiration rates and even for fruits with high water loss such as yucca. In this fruit, 82% of the water is imported via xylem, with 89% transpired (van Die and Willemnse, 1980). Thus, the phloem supplies both water and dry matter for fruit growth in a wide range of crops. Changes in leaf:fruit ratio affect the relative supply of carbohydrates available for fruit growth (Chacko *et al.*, 1982) and dry matter content (Simmons *et al.*, 1998). These changes would be expected to alter water and dry matter accumulation. When examining the water and dry matter accumulation from the point of view of fruit quality, we must consider the various fruit components.

In mango fruit, which is a drupe, the peel, pulp and stone each have specific functions and compositions and also appear to accumulate water and dry matter at different rates. The thick peel protects the fruit from external agents and consists primarily of epidermal cells and a cuticle layer covered by wax. The peel contains more phenols and cellulose composites than the pulp (Leley *et al.*, 1943). Peel cells have limited water uptake and tissue expansion compared to the pulp. The pulp is normally sweet and succulent in commercial cultivars. The large parenchyma cells in the pulp store water and sugars as the fruit expands (Mukerjee, 1959). The stone protects the seed and prevents it from drying. The stone contains the largest quantities of lipids and lignin. It is soft during the first half of fruit development and then hardens. It may loose water at this stage.

The aim of this paper was to examine changes in water and dry matter accumulation during mango (*Mangifera Indica* L. cv. 'Lirfa') fruit growth over a single season in Reunion Island. Different leaf:fruit ratios (10, 25, 50, 100 and 150 leaves per fruit on girdled branches) were used to modify the relative supply of carbohydrates to the fruit. The water and dry matter contents of the different components of the fruit were examined.

TABLE I:

Effects of leaf:fruit ratio on final dry and water weights of the various fruit components (peel, pulp and stone). Values are the means of six fruits per treatment harvested at the final date of the experiment. Values with different letters within columns are significantly different at $P < 0.05$.

	Leaf:fruit ratio	Peel	Pulp	Stone
Dry weight	10	7.78^{a}	31.25^{a}	13.09^{a}
	25	10.44^{ab}	51.59^{ab}	18.13^{abc}
	50	12.97^{bc}	64.26^{bd}	19.11^{bc}
	100	17.70^{c}	96.43^{c}	22.80^{bc}
	150	17.20^{c}	85.61^{cd}	18.60^{bc}
		***	***	***
Water weight	10	24.91^{a}	177.66^{a}	20.54^{a}
	25	28.59^{ab}	241.20^{ab}	23.27^{a}
	50	33.26^{bc}	280.62^{b}	26.18^{ab}
	100	38.04^{c}	379.51^{c}	32.72^{b}
	150	37.90^{c}	362.29^{c}	28.32^{ab}
		***	***	***

*** F test significant at $P < 0.001$ (global effect of the treatment)

1.2 Materials and methods

1.2.1 Material and treatments

The experiment was conducted on 11-year-old trees of cv. 'Lirfa', grafted on 'Maison Rouge', in Réunion Island (20°52'48''S, 55°31'48''E). The trees were planted in ten rows, 7 m apart, with nine trees each(3 m high), spaced 5 m apart. Trees received 100 kg N ha^{-1} (urea), 20 kg P ha^{-1} (superphosphate) and 100 kg K ha^{-1} (potassium sulphate) in March 2000 and after harvest, and 200 kg N ha^{-1} (urea), 20 kg P ha^{-1} (superphosphate) and 100 kg K ha^{-1} (potassium sulphate) on October 2000 (early fruit growth). Trees were irrigated every two days to replace potential evapotranspiration. Data from eight linear variable displacement transducers (LVDT, Solartron, UK) showed that daytime shrinkage was less than 20 µm for 3 to 4 cm thick stems, indicating that the trees were well watered.

Six weeks after flowering, two hundred and fifty branches were chosen on twenty-three trees. Branches were ramified with different shoots of the current year and the previous one. Their position was randomly chosen on the top of the tree to reduce the variability of light received by leaves which could significantly change carbon assimilation and fruit growth as well. About ten to fifteen branches per tree were used for this experiment representing less than 1/10 of the total branches on the tree canopy. After the branches were chosen, they were girdled and sometimes defoliated to give 10, 25, 50, 100 and 150 leaves per fruit (with 50 leaves for 5 fruits, 100 leaves for 4 fruits, 100 leaves for 2 fruits, 100 leaves for 1 fruit and 150 leaves for 1 fruit, respectively). Branches were girdled by making a 10 to 15 mm cut through the bark to the cambium. To keep the leaf:fruit ratios constant within each treatment, new leaves were removed. The trees in this orchard were homogeneous and grown in the same environment (climatic conditions and cultural practices). This indicated that there was no tree effect on fruit growth of isolated branches which was confirmed by the results of a randomised analysis of variance (treatment x time x tree; not shown).

1.2.2 Data collection and analyses

Six fruits from each treatment (leaf:fruit ratio) were harvested each week for two months after girdling. For each fruit, the total fresh weight and that of its components (peel, pulp and stone) was measured. Samples were then dried at 75°C for 48 h, and the corresponding dry weights recorded. The absolute water weight (WW) of the various components was calculated as the fresh weight (FW) minus the dry weight (DW). The relative dry matter content, in %, was calculated as the ratio between the dry weight and the fresh weight. The sum of growing

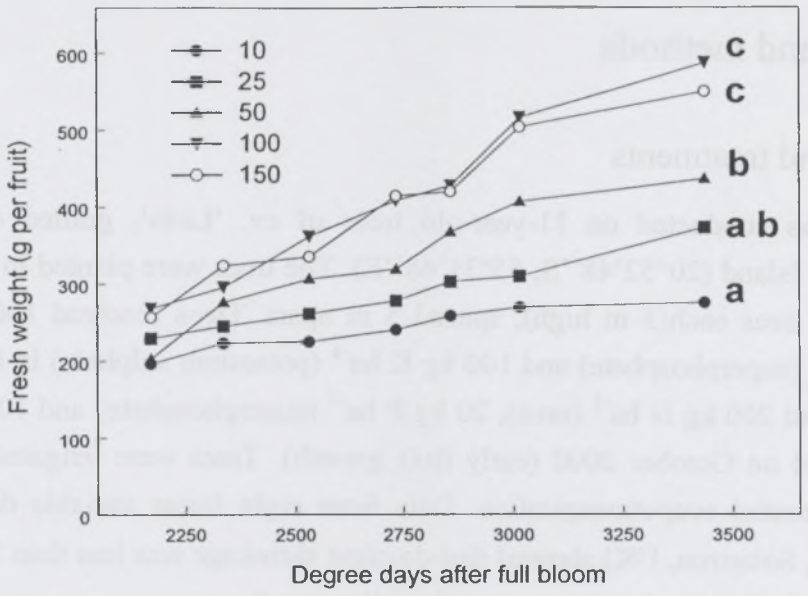

Figure 1: Effects of leaf:fruit ratio on the growth of mango fruits expressed as fruit fresh weight. Data points are the mean values of six fruits per treatment. Different letters mean that final fruit weight is significantly different at $P < 0.05$.

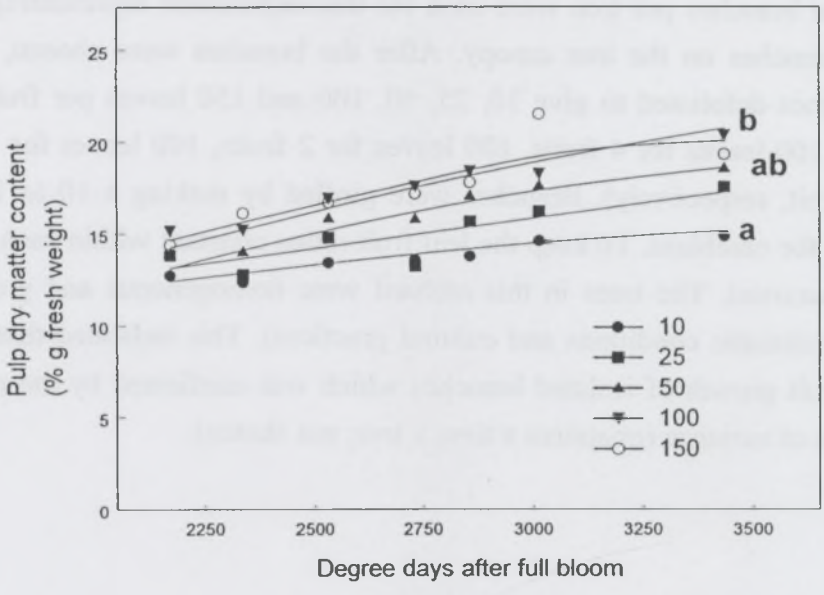

Figure 2: Effects of leaf:fruit ratio on the pulp dry matter content (in %). Data points are the mean values of six fruits per treatment. Lines represent a data smoothing of the pulp dry matter content calculated with Equation 1 and the measurements of fruit dry weight, for each treatment.

degree days was calculated by adding up the average daily temperatures during the growing season.

Relationships between water and dry weights of the whole fruit and those of its components were assessed by power functions. Parameters of the different relationships were estimated by non-linear regression. Each equation was log-transformed to calculate the coefficient of determination R^2 and to perform an F-statistic test in order to examine the significance of the regression.

To analyse if equations of pulp and peel dry weight as a function of fruit dry weight were different from those of water weight, the likelihood ratio test with an asymptotic level of 95% was used, based on the results of the non-linear regressions (Huet *et al.*, 1996). This type of test makes it possible to compare nested models. The simple model with the same parameters for water and dry weights was compared to complex models in which parameters were different. The effect of treatment (leaf:fruit ratio) was analysed at harvest by analysis of the variance of data related to the fruit fresh weight, the pulp dry matter content and the water and dry weights of the various components. In the case of a significant effect, Tukey's multiple comparison test was performed to determine which treatments were significantly different at the 0.05 level.

1.3 RESULTS

Fruit fresh weight increased with time (Figure 1). Fruit from branches with 100 or 150 leaves per fruit were larger than those with 10, 25 or 50 leaves per fruit. At 3500 degree days, fruit fresh weight on Treatment 100 and 150 was about 550 g. At this stage, it was possible to harvest these fruits that had already begun to ripen. On the other hand, on Treatment 10, fruits had 250 g of fresh weight, their skin colour had not changed and they were often green. There was also a significant difference between branches with 10 and 50 leaves per fruit.

There was also a significant effect of the leaf:fruit ratio on the pulp dry matter content (Figure 2). The pulp dry matter content was greater in fruits of Treatment 100 - about 20%, as opposed to 14% in Treatment 10.

The final dry and water weights of each component were significantly affected by the leaf:fruit ratio (Table I). In the three components, the water and dry weights were greater in fruits of Treatment 100 than in Treatment 10. There was also a significant difference of dry and water weights in the pulp between Treatment 100 and Treatment 25 or 50. Larger fruit, on Treatment 100, had a greater proportion of final fruit dry weight in the pulp (70.4%) than smaller fruit on Treatment 10 (60.0%). As for dry weight, the proportion of final fruit water weight was higher in the pulp and lower in the stone and in the peel in the highest leaf:fruit ratio than in the lowest leaf:fruit ratio.

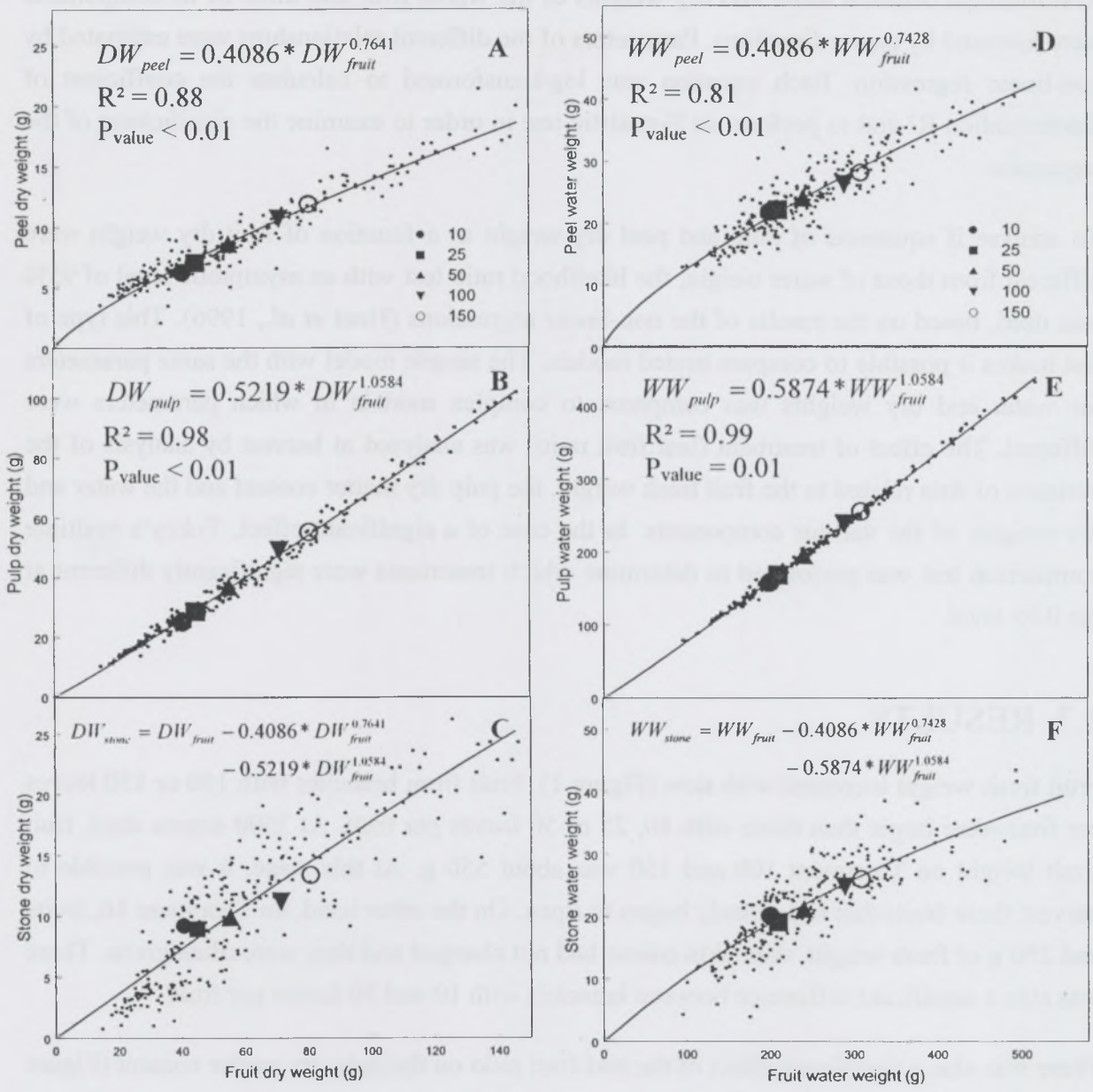

Figure 3: Relationships between dry weight (DW) or water weight (WW) in the various components of mango fruit and corresponding fruit weight. The relationships concern the peel (A, D), the pulp (B, E) and the stone (C, F), in relation to the whole fruit. Small points indicate all measurements of the five treatments (seven dates of harvest and six repetitions per treatment). The five bigger symbols are mean values of all of the measurements of each of the five treatments.

There were strong relationships between the dry weight of the various fruit components and the total fruit dry weight (Figures 3A, 3B, 3C). For each treatment, the dry weights of the various components were accurately distributed along the fitted curves. All these relationships were independent of the leaf:fruit ratio. As the fruit developed, about 12 to 20% of the fruit dry weight was in the peel, 60 to 70% in the pulp and 18 to 20% in the stone. However, there was a small gap between the stone weight and the fitted model (Figure 3C) during early fruit growth. When the data were analysed on a water weight basis, similar relationships were found (Figure 3D, 3E, 3F). Nevertheless, results of the likelihood ratio test have shown that this second set of equations was significantly different with relationships concerning dry weight. The model that accurately described measurements was not the complex model in which all parameters are different but, rather, an intermediate model with several equal parameters for the relationship concerning dry weight and that of water weight. About 8 to 13% of the fruit water weight was in the peel, 78 to 86% in the pulp and 6 to 9% in the stone. The peel and the stone component were relatively low when expressed on a water weight basis rather than on a dry weight basis because of the higher fruit water weight in the pulp.

Regardless of the treatment, there was a strong correlation between the water and dry weight of each of the fruit components (Figure 4). All the exponents of the relationships were lower than one. Therefore, the rate of water accumulation in each component decreased when the dry weight increased. This rate was higher in the pulp followed by the peel and the stone. In this last component, the fitted curve (Figure 4C) showed that its water weight increased quickly during the first part of growth. Then, for a stone dry weight bigger than 7.5 g, this component accumulated more dry matter than water, while, the two other components often accumulated more water than dry matter during fruit development.

With the different relationships (see Figures 3 and 4), it was possible to calculate the dry matter content of the various components on the basis of the fruit dry weight. For the pulp, we obtained:

$$\%DW_{pulp} = \frac{DW_{pulp}}{FW_{pulp}} * 100 = \frac{DW_{pulp}}{DW_{pulp} + WW_{pulp}} * 100 = \frac{100}{1 + 26.0937 * \left(DW_{fruit}\right)^{-0.3888}} \qquad (1)$$

Figure 2 shows that the prediction of the seasonal variation of dry matter content in the pulp, using Equation 1 and measurements of fruit dry weight, was accurate.

1.4 DISCUSSION

In the present study, it was shown that increasing the number of leaves per fruit affected mango fruit growth (cv. 'Lirfa') by improving fruit size at harvest, as reported earlier for other cultivars by Chacko *et al.* (1982) and Reddy and Singh (1991). Fruits of treatments with 100

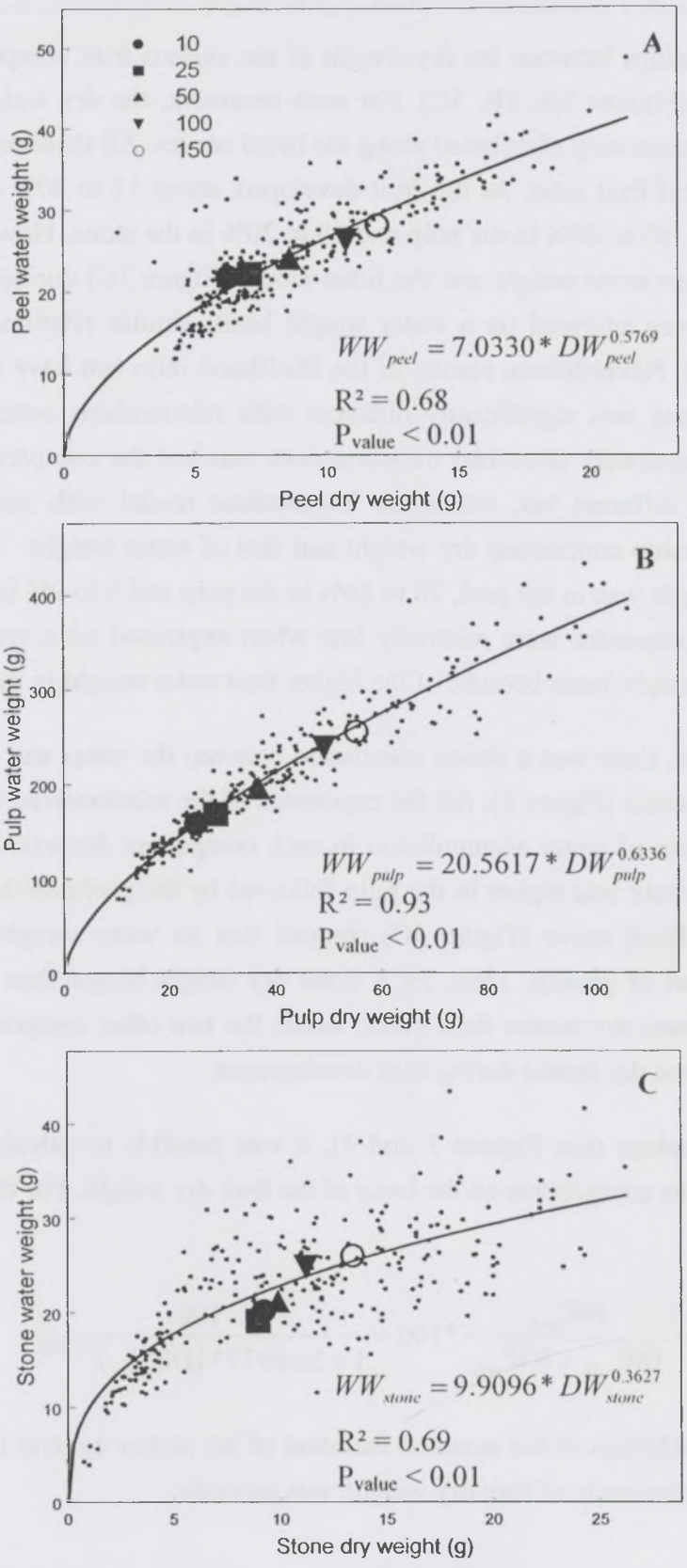

Figure 4: Relationships between water weight (WW) and dry weight (DW) in the peel (A), the pulp (B) and the stone (C). Small points indicate all of the measurements of the five treatments (seven dates of harvest and six repetitions per treatment). The five bigger symbols are mean values of all of the measurements of each of the five treatments.

leaves per fruit had the highest weight, implying that thinning mango trees could be advantageous for improving fruit size. Moreover, since mango fruit development utilizes both reserves and current photosynthesis carbohydrates (Chacko *et al.*, 1982), larger amounts of carbohydrates are withdrawn for fruit growth when there are just 10 leaves per fruit. Therefore, increasing the leaf:fruit ratio could make it possible to accumulate starch reserves for vegetative growth and fruiting in the following season (Chacko *et al.*, 1982).

Chauhan and Pandey (1984), who measured ^{14}C-sucrose translocated from leaves to mango fruits at different stages of growth, found that the majority of this ^{14}C-sucrose accumulated in the pulp. This is in agreement with our results on dry weight. The stone had the particularity of storing relatively more dry matter than water in the second half of fruit growth, during the stone hardening phase. During early fruit growth, there was a small gap between stone weight and the fitted model (Figure 3C). At this stage, the endocarp was thin and could not be easily separated from the pulp. We may have underestimated the weight of the stone.

We also found that the accumulation of water and dry matter changed over time and as a function of leaf:fruit ratio as well. These changes of water and dry weights were accurately estimated each one by a unique relationship, regardless of the treatment. The rate of water accumulation decreased as dry weight increased. Moreover the dry matter content increased as the fruit developed and fruits on branches with a high leaf:fruit ratio such as 100 and 150 leaves per fruit, had the greatest pulp dry matter content. These changes indicate that the treatment affected dry matter supply more than water supply. Similar increases in dry matter content with higher leaf:fruit ratio were observed for cv. 'Kensington' mango fruit on branches by Simmons *et al.* (1998). Pulp dry matter content is linked to quality traits (Diczbalis *et al.*, 1995; Richardson *et al.*, 1997), so higher leaf to fruit ratios improved mango fruit quality (Simmons *et al.*, 1998). However, other traits of fruit quality such as sugars, acids or Ca concentrations should be taken into account in order to give a more precise view of the effect of leaf:fruit ratio on the quality and the storage performance of mango fruit. These results are interesting for the mango industry in Réunion Island and could lead to higher yields and the improvement of fruit quality.

The estimation of pulp dry matter content is very useful. As described in Equation 1, it just depends on the fruit dry weight. Fruits from the highest leaf:fruit ratio reached maturity before fruits in the other treatments. Pulp dry matter content could become an indicator of when to harvest mango fruit, as is the case in other countries (Diczbalis *et al.*, 1995).

2 Leaf to fruit ratio and irrigation supply affect seasonal changes in minerals, organic acids, and sugars of mango fruits

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Running title : Seasonal variations of quality in mango

Soumis à *Journal of the Science of Food and Agriculture*

Abstract

To determine the effects of assimilate and water supply on the determination of mango fruit quality, the seasonal variation of minerals, acids, and sugars were investigated during two successive years. To manipulate the assimilate supply, selected branches were girdled to provide 10, 25, 50 and 100 leaves per fruit. Irrigation was managed to provide two levels of water supply conditions. Fruit growth rate was greater with increasing leaf to fruit ratio. Total dry matter content of flesh was higher in fruit with higher leaf to fruit ratio. No effect was found on structural dry matter content of flesh. Potassium and magnesium concentrations were not affected by the leaf to fruit ratio whereas calcium, transported via xylem, had a higher concentration in flesh fruit from low leaf to fruit ratio, as 10 leaves per fruit. Low assimilate supply increased malic and citric acid concentrations. Glucose remained almost constant during fruit development regardless treatments. Fructose accumulated at higher rates when assimilate supply was lower. Sucrose concentration was significantly increased by higher leaf to fruit ratio. Close to maturity, levels of sucrose storage and starch breakdown were positively correlated with assimilate supply. Levels of starch breakdown were correlated with irrigation supply. This gradient of sugars and acids according to treatments may changed fruit taste.

Keywords : *Mangifera indica*, mango, leaf to fruit ratio, irrigation, fruit composition, quality, structural material.

2.1 Introduction

The taste of fruit flesh depends greatly on the balance between soluble sugars and organic acids. In mango flesh, the predominant acids are citric and malic acids, while the major sugars are sucrose, fructose and glucose (Medlicott and Thompson, 1985). The overall sweetness of fruit flesh is highly dependent on the composition of its sugars. Mango fruit would be of good taste if its flesh stored large amounts of sucrose and fructose. Indeed fructose is 2.3 and 1.7 times sweeter than glucose and sucrose, respectively (Kulp *et al.*, 1991). The sweetness, however, is also affected by the composition of acids. Citric acid may decrease the sweetness of sucrose (Bonnans and Noble, 1993), while malic acid may decrease that of fructose (Fabian and Blum, 1943). The acidity of mango flesh falls, while the total soluble sugar level increases with maturity (Wahab and Khan, 1954). Loss in acidity during ripening is indicated by decreased citric acid content. The reduction in starch, and the increase in sucrose, sometimes glucose and fructose, during ripening make the fruit less sour (Selvaraj *et al.*, 1989). Fruit maturation, another trait of fruit quality, may be evaluated by the patterns of different biochemical compounds such as starch or sucrose (Akamine and Goo, 1973; Krishnamurthy and Subramanyam, 1970; Mendoza and Wills, 1984). From these studies a consistent pattern of fruit maturation emerges whereby the starch content drops is followed by a strong increase in sucrose and consequent sweetness (Tandon and Kalra, 1983).

In the tissue of many fruits including mango, calcium concentration or concentration ratios of calcium to other minerals such as potassium and magnesium has been reported as important factors governing fruit storage quality. Calcium is one of the minerals believed to contribute to delay ripening, senescence (Ferguson, 1984), and to reduce storage disorders (Bangerth, 1979). Physiological disorders such as soft-nose in mangoes have been found to be associated with low calcium levels in fruits, which may damage the structure integrity of cell walls during fruit softening. Changes in flesh composition of mango fruit associated with ripening were the predominant subject of many studies dealing with quality. Only a few studies, to our knowledge, have evaluated mango fruit flesh composition all along the growth and the maturation, which determines the quality at harvest.

The elaboration of gustatory quality, the maturation (Souty *et al.*, 1999) and the shelf life (Simmons *et al.*, 1998) are linked to fruit growth. Various orchard management practices affect fruit growth by changing assimilate supply and water availability. The effect of assimilate supply was studied by analysing the effect of leaf to fruit ratio on water and dry matter contents in mango fruit (Léchaudel *et al.*, 2002). Mango fruit size decreases with decreasing leaf to fruit ratio (Chacko *et al.*, 1982), probably due to the limited availability of assimilates. Low leaf to fruit ratio on peach reduced fruit growth rate, sweetness of the fruit, and delayed fruit maturity as indicated by a latter rise of ethylene production (Souty *et al.*, 1999). At harvest the worst eating quality of fruit developed with reduced crop load was due

to lower sucrose and hexose sugars content (Bertin *et al.*, 2000) and higher levels of citric acid (Wu *et al.*, 2002). However, these fruits contained the highest calcium and the lowest potassium concentrations (Volz *et al.*, 1993) which has a positive effect on fruit storage and reduced disorders.

Response of trees to water stress depends on the stages of the fruit growth, the frequency, the severity of the stress and also the cultivars. Water stress during the cell division phase affects dramatically potential fruit size in apple (Naor *et al.*, 1995) and nectarine (Berman and Dejong, 1996). Reducing irrigation in the early growing season or during the entire season decreases harvest weight whereas increases soluble sugars concentrations and acidity in pear (Ramos *et al.*, 1994), apple (Kilili *et al.*, 1996; Mills *et al.*, 1996), citrus fruits (Gonzàlez-Altozano and Castel, 1999) and kiwifruit (Miller *et al.*, 1998). Pear fruits tended to have lower calcium concentration and higher storage disorders when they were exposed to water stress at early season (Behboudian *et al.*, 1994). Water stress applied later in the season have less impact on fruit size and improved quality attributes either by advancing maturity in kiwi (Miller *et al.*, 1998) or by increasing sugar concentration and fruit storage quality in apple (Mpelasoka *et al.*, 2001).

Biochemical compounds of fruit flesh linked to quality components were generally investigated in concentration of a certain compound (g) per kg of fresh weight. However changes in the concentration expressed per fresh weight can be influenced by several factors such as dilution, amount of cell wall material produced and the transport-metabolism process of minerals, acids, and sugars, which may be differently sensitive to water and assimilate supply. Fresh flesh is composed of water and dry matter. The latter is composed of structural dry matter, such as cell walls, cellulose, and the non structural dry matter, like soluble sugars, acids, minerals and starch.

To better understand which of these components are affected by water and assimilate supply, we propose to analyse changes in: total dry matter content (total dry weight/total fresh weight), structural dry matter content (structural dry weight/total dry weight), and concentration of individual non-structural compound per structural dry weight of flesh. In this study the structural dry weight of the flesh was calculated as the difference between the total dry weight of the flesh and the sum of the dry weights of all the non-structural components. The seasonal changes of the main quality components of fruit flesh, such as fruit weight, dry matter content of fruit flesh, and the concentrations of minerals, acids, and sugars, were assess in relation to assimilate and water supply during two successive years.

2.2 Materials and methods

2.2.1 Experimental conditions and treatments

This study was conducted on 11-year-old mango trees of cv. 'Lirfa', grafted on 'Maison Rouge', in La Réunion island (20°52'48''S, 55°31'48''E) during the 2000 and 2001 growing seasons. The 2000 experimental plot consisted of ten rows, 7 m distant, each of them made of nine trees spaced 5 m apart, and about 3 m high. The trees observed in 2001 were spaced at 5 m by 6 m and were around 3 m high in an adjacent plot.

During the 2000 growing season, all trees were well irrigated every two days at 100 % replacement of evaporation. Data from eight linear variable displacement transducers (LVDT, Solartron, UK) showed that daytime shrinkage was less than 20 µm for branches with diameter of 3-4 cm, indicating that the trees were well watered. Six weeks after flowering, 250 branches were chosen on twenty-three trees. Branches were ramified with different shoots of the current year and the previous one. Their position was randomly chosen on the top of the tree to reduce the variability of light received by leaves which could significantly change carbon assimilation and fruit growth as well. About ten to fifteen branches per tree were used for this experiment, which represented less than 10 % of the total branches on the tree canopy. After the branches were chosen, they were girdled, sometimes defruited and defoliated to give 25, 50 and 100 leaves per fruit (with 100 leaves for 4, 2 and 1 fruit respectively). Branches were girdled by removing a band of bark of 10-15 mm wide. To keep the leaf to fruit ratios constant within each treatment any new emerging leaves were removed.

During the 2001 growing season, two irrigation treatments were applied: control irrigation (CI) and no irrigation (NI) treatments. The CI trees were well-irrigated with as in 2000. In the NI treatment, irrigation was completely withheld one month after full bloom. These trees received just water coming with the rainfall, about 170 mm from the beginning of the irrigation stop to the end of the fruit growing season. It represented 24 % of the total water received by trees from CI treatment. Trees were divided into six blocks of nine trees. Thus, eight neighbours of the studied tree had the same irrigation treatment. Three blocks received the same irrigation treatment. Six weeks after flowering, the branches chosen with the same precaution as in 2000 were girdled, sometimes defruited and defoliated to get 10 and 100 leaves per fruit (with respectively 50 leaves for 5 fruits and 100 leaves for 1 fruit).

2.2.2 Measurements of fruit composition

During the 2000 growing season, six fruits from each treatment (three leaf to fruit ratios: 25, 50, 100) were harvested each week between 15 November 2000 to 4 January 2001. In the second year of experiment, six fruits of each treatment (two leaf to fruit ratios, 10 and 100,

Table 1: Analysis of variance for mango fresh flesh weight (g), total dry matter content (%) and structural dry matter content of the flesh

Year	Factors	Mean square and F significance		
		Fresh flesh weight	Total dry matter content	Structural dry matter content
2000	Age (A)	67257***	43.6***	0.0164***
	Leaf/fruit (LF)	129047***	68.7***	0.0025 n.s
	A x LF	6073***	1.5 n.s	0.0053 n.s
2001	Age (A)	107271***	229.9***	0.2697 n.s
	Leaf/fruit (LF)	230180***	289.8***	0.0031 n.s
	Irrigation (I)	3 n.s	19.5*	0.0007 n.s
	A x LF	8523***	12.9**	0.0045 n.s
	A x I	1276 n.s	6.1 n.s	0.0070 n.s
	LF x I	3532 n.s	3.8 n.s	0.0452***
	A x LF x I	2368 n.s	6.2 n.s	0.0013 n.s

Non-significant (n.s)
* significant at P<0.10.
** P<0.05.
*** P<0.01.

with each of CI and NI) were harvested every fifteen days between 19 October 2001 to 21 January 2002. For each fruit, the fresh weight and the flesh weight were measured. A sample of fresh flesh was taken from each fruit, weighted, and then dried at 75°C for 48 h, and the corresponding dry weights recorded, whereas the remainder was frozen at -20°C for future analysis. The relative dry matter content, in %, was calculated as the ratio between the dry weight and the fresh weight of the flesh. The structural dry matter content was the ratio between the structural dry weight and the total dry weight of the flesh. The structural dry weight was determined as the difference between the total dry weight of the flesh and the sum of dry weights of non-structural components.

For analyses in the 2000 growing season, the frozen flesh pulp was defrozen, homogenised and centrifuged to extract the crude juice. Concentrations of calcium, magnesium and potassium were determined on the diluted mango juice with a capillary ion analysis (CIA) using a Waters's instrument (Waters, Massachusetts, USA). The CIA conditions were UV CAT2 electrolyte, silica capillary, 10-µA current and 20kV voltage, hydrostatic injection, 10 nL sample injected, Electro-osmotic flux migration, and UV detection (185 nm, mercury lamp). Concentrations of organic acids were also determined using the Water's CIA instrument based on the Laksaridou-Monnerville's method (Laksaridou-Monnerville, 1997) using diluted mango pulp. Briefly, the CIA conditions were Phosphate 7.5µM/OFM-OH electrolyte, silica capillary 75µm x 60cm, 7-µA current and 17kV voltage, hydrostatic injection, 10 nL sample injected, electro-osmotic flux migration, and UV detection (185 nm, mercury lamp). Concentrations of sucrose, glucose and fructose were measured using a high-performance liquid chromatography (HPLC) system (DIONEX Co., Sunnyvale, USA). The HPLC conditions were CarbopacPA1 guard-column and column, 25µL sample injected, isocratic elution by a 200mM NaOH and purified water mixture (85:15, v/v), flow rate at 1 mL/min, and amperometric detection (type ED40). Peaks of sugars were confirmed by comparison to standard solution. Starch was hydrolysed with amyloglucosidase (14 amyloglucosidase units/ml, Novo Nordisk Bioindustries Ltd., Denmark) and its concentration was determined by a colorimetric dosage of glucose (glucose analysis kit, ref 716251/Boehringer Mannheim, Diffchamb, France).

In the 2001 growing season, the fresh pulp was defrozen and finely homogenised by a Polytron (PT1600E, Kinematica AG, Switzerland). The sugars, starch, and minerals were analysed as in 2000. The concentrations of organic acids were analysed by using a HPLC method. The conditions were CarbopacPA1 guard-column, IonPacAS11 column, 25µL sample injected, elution by a linear gradient from 0.5mM to 35mM NaOH in 25min, flow rate at 2 mL/min, and conductimetric detection (type ED40 equipped with an automatic suppressor: ASRS cartridge). Peaks of organic acids were confirmed by comparison to standard mixture.

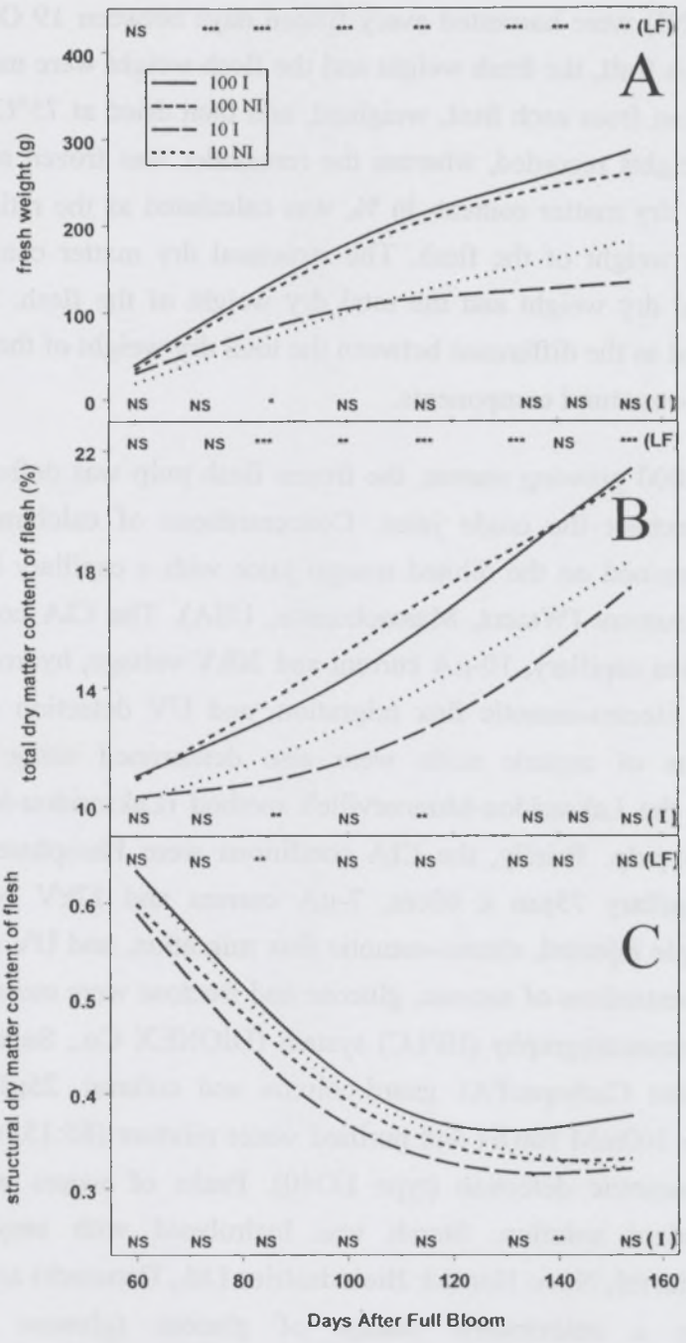

Figure 1: Seasonal variation of mango fruit growth, total dry matter content, and structural dry matter content of the fruit flesh during the 2001 experimental period. The label 10 and 100 indicated the leaf to fruit ratio. I and NI indicate well-irrigated and no irrigated treatments. Differences between the leaf to fruit ratio (LF) or between the irrigation treatment (I) were either significant at P<0.10 (*), P<0.05 (**) or P<0.01(*) or non-significant (NS) on each sampling date. Levels of significance of the difference was shown at the top of each figure (LF) and at the bottom (I). All the curves were smoothed using the 'loess' method (Splus, statistical software, MathSoft Inc., Cambridge, MA).

2.2.3 Statistical analysis

An analysis of variance was performed on observed fresh mass, total dry matter content, structural dry matter content, and concentrations of the non-structural components of the flesh, from the two years of experiments to study the effects of fruit age, assimilate supply, water supply and their two- or three-way interactions. As the period of sampling dates was longer during the second than the first year of experiment, an analysis of variance was carried out on each sampling dates with leaf to fruit ratio (LF) and irrigation (I) as factors.

2.3 Results

Both fresh flesh weight, total dry matter content and structural dry matter content of the flesh were significantly influenced by fruit age (days after full bloom) in 2000 and 2001 (Table 1). In 2001 fruit flesh weight increased almost linearly until 100 days after full bloom and then tended to slow down (Figure 1A). The total dry matter content increased with the fruit development (Figure 1B). The structural dry matter content of the fruit flesh decreased rapidly until 120 days after full bloom and then stayed nearly constant (Figure 1C). The effects of leaf to fruit ratio on the fresh flesh weight and the total dry matter content of the flesh were significant in both years of experiment (Table 1). An increase of the leaf to fruit ratio strongly increased fruit size and total dry matter content of the flesh in 2001 (Figures 1A and 1B). At maturity, the latter was about 20 % higher in treatment 100 leaves per fruit than in treatment 10. In 2001, total dry matter content of the flesh was also affected by tree irrigation (Table 1). Reducing irrigation seemed to increase it (Figure 1B). Neither irrigation nor assimilate supply had significant effect on the structural dry matter content of the flesh (Table 1) but their interaction had some.

Flesh composition, such as minerals, organic acids and sugars were affected by fruit age during the two years of experiment (Table 2). Seasonal trends in 2000 were similar to those in 2001 (data not shown). K represented more than 80 % of the pool of cation in mango fruit flesh followed by Ca and Mg (Figure 2). In 2001, K concentration increased slightly with fruit development between 0.015 to 0.030 g per g of structural dry weight (Figure 2A) whereas Mg and Ca concentrations tended to decrease during fruit development (Figures 2B and 2C). The effect of leaf to fruit ratio was particularly strong on Ca in the two years of experiment (Table2). Ca concentration was higher in fruit flesh with low leaf to fruit ratio. The effect of assimilate supply (leaf to fruit ratio) on Mg was less marked. No treatment effect was found on K concentration, however there was an interaction effect between leaf to fruit ratio and tree irrigation.

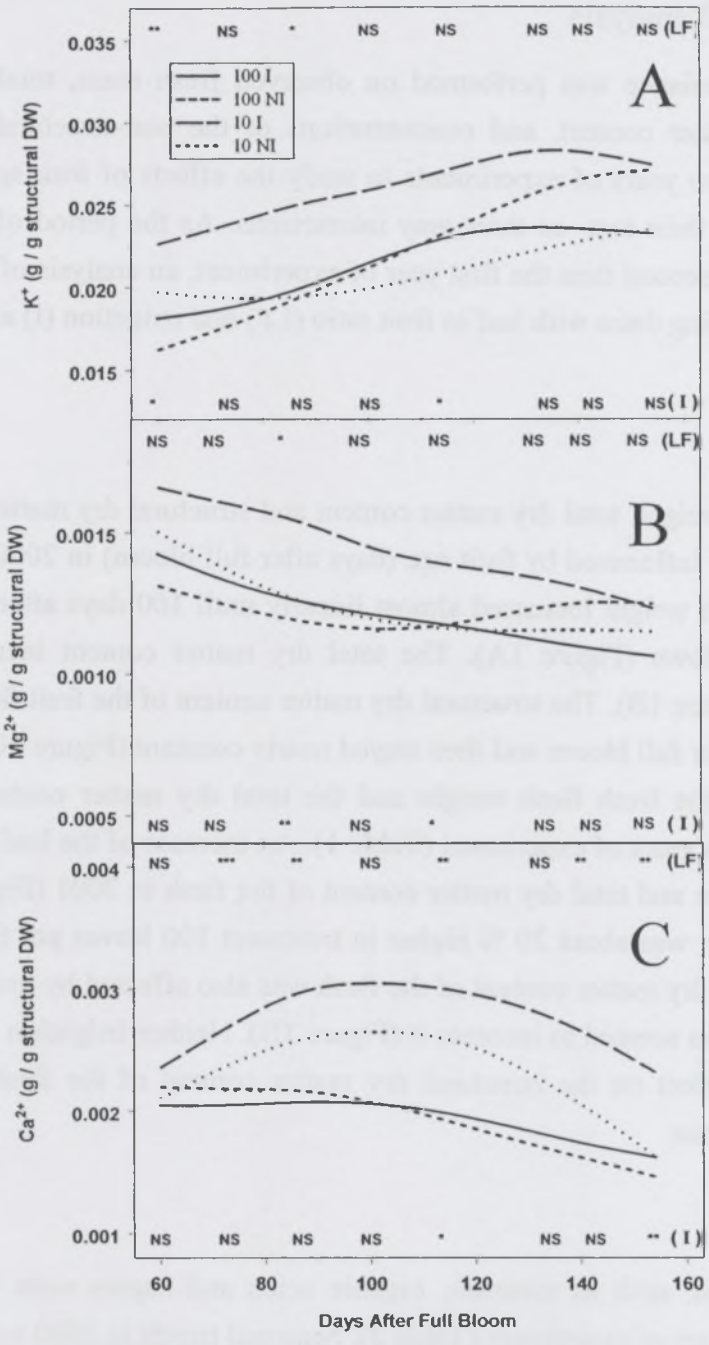

Figure 2: Seasonal variation of potassium (K^+), magnesium (Mg^{2+}), and calcium (Ca^{2+}) concentrations in g per g of structural dry weight during the 2001 experimental period. The label 10 and 100 indicated the leaf to fruit ratio. I and NI indicate well-irrigated and no irrigated treatments. Differences between the leaf to fruit ratio (LF) or between the irrigation treatment (I) were either significant at $P<0.10$ (*), $P<0.05$ (**) or $P<0.01$(*) or non-significant (NS) on each sampling date. Levels of significance of the difference were shown at the top of each figure (LF) and at the bottom (I). All the curves were smoothed using the 'loess' method (Splus, statistical software, MathSoft Inc., Cambridge, MA).

Citric acid increased until 90 days after full bloom to reach a maximum about 0.35 to 0.50 g per g of structural dry weight according to treatments, and afterwards decreased gradually to below 0.1 (Figure 3A). In contrast malic acid concentration decreased continuously from 0.5-0.1 g per g of structural dry weight to a minimum concentration of less than 0.037 at the time of about 100 days after full bloom (Figure 3B). Then during the last month, there was a graduate and small increase. Malic and citric concentrations were significantly affected by leaf to fruit ratio (Table 2). Citric and malic acid concentrations were higher almost all along the fruit development from the lower leaf to fruit ratio (Figures 3A and 3B) even if difference between treatments decreased as fruit developed. Irrigation treatment did not affect acid concentration (Table 2).

Soluble and insoluble sugars had different seasonal trends. The minor in concentration, glucose was the only to decrease during the majority of the time of fruit development (Figure 4A). The concentration of fructose increased steadily all along fruit development to reach the peaks at fruit maturity between 0.3 to 0.5 g per g of structural dry weight according to treatments (Figure 4B). Sucrose concentration remained low, around 0.25 g per g of structural dry weight until 100 days after full bloom, then it increased and could rise up a concentration about 1.25 g per g of structural dry weight at the end of fruit growth (Figure 4C). Glucose and fructose concentrations were significantly affected by assimilate supply the two years of experiment (Table 2). Lower leaf to fruit ratio (10 leaves per fruit) significantly increased glucose and fructose concentrations until 120 days after full bloom for glucose (Figure 4A), and all along fruit development for fructose (Figure 4B). Sucrose concentration was higher in fruits with higher leaf to fruit ratio during the latter stage of fruit development (Figure 4C). Furthermore, an interaction between leaf to fruit ratio and tree irrigation was found on the three soluble sugar concentrations (Table 2). The seasonal trend of starch concentration could be separated in two phases (Figure 4D). During the first phase, starch concentration increased to reach a maximum about 1.0 to 1.2 g per g of structural dry weight according to treatments. Then, it decreased rapidly to about 0.2 g per g of structural dry weight towards the end of fruit development. From 130 days after full bloom onwards, starch seemed to be affected by leaf to fruit ratio (Table 2 and Figure 4D). During the period near maturity, fruit flesh from treatment with higher assimilate supply had more sucrose and less starch than low leaf to fruit ratio. Water stress enhanced the difference, especially for starch. For the same leaf to fruit ratio, starch concentration was higher in water stressed trees (Figure 4D). Moreover, starch breakdown occurred later in the fruit flesh from treatment with less assimilate and water supply.

Table 2: Analysis of variance for mango flesh composition in minerals, organic acids and sugars (in g per g of structural dry weight)

Year	Factors	Mean square and F significance								
		K	Mg	Ca	Malic acid	Citric acid	Glucose	Fructose	Sucrose	Starch
2000	Age (A)	42.10-6 *	10.10-8 *	7.10-7 **		0.026 ***	0.0126 ***	0.007 **	0.018 **	0.450 ***
	Leaf/fruit (LF)	8.10-6 n.s	6.10-8 n.s	11.10-7 **		0.013 *	0.0029 ***	0.017 ***	0.027 **	0.026 n.s
	A x LF	33.10-6 n.s	5.10-8 n.s	1.10-7 n.s		0.008 **	0.0004 n.s	0.004 n.s	0.006 n.s	0.085 n.s
2001	Age (A)	236.10-6 ***	52.10-8 ***	32.10-7 ***	0.0129 ***	0.439 ***	0.0234 ***	0.162 ***	2.915 ***	3.276 ***
	Leaf/fruit (LF)	110.10-6 n.s	83.10-8 **	168.10-7 ***	0.0142 ***	0.140 ***	0.0240 ***	0.248 ***	0.601 ***	0.030 n.s
	Irrigation (I)	181.10-6 *	37.10-8 n.s	18.10-7 *	0.0007 n.s	0.034 n.s	0.000014 n.s	0.001 n.s	0.008 n.s	0.0002 n.s
	A x LF	64.10-6 n.s	10.10-8 n.s	13.10-7 *	0.0030 **	0.042 ***	0.0041 ***	0.010 n.s	0.165 ***	0.242 **
	A x I	56.10-6 n.s	30.10-8 *	5.10-7 n.s	0.0008 n.s	0.009 n.s	0.0008 n.s	0.014 n.s	0.015 n.s	0.333 ***
	LF x I	410.10-6 ***	57.10-8 *	17.10-7 n.s	0.0022 n.s	0.055 **	0.0100 ***	0.037 *	0.383 ***	0.064 n.s
	A x LF x I	70.10-6 n.s	27.10-8 n.s	6.10-7 n.s	0.0014 n.s	0.019 n.s	0.0010 n.s	0.0136 n.s	0.090 ***	0.098 n.s

Non-significant (n.s)
* significant at P<0.10.
** P<0.05.
*** P<0.01.

2.4 Discussion and conclusion

2.4.1 Fruit composition and seasonal changes

The relative importance in the concentration of minerals (i.e K > Ca > Mg) in mango fruit flesh, similar as in apples (Jones *et al.*, 1983) or in Asian pear (Behboudian *et al.*, 1994), was maintained during fruit development because of the seasonal increase of K while the two other tended to decreased. The seasonal parabolic trend of citric acid in mango flesh is similar to those obtained for various species such as peach (Wu *et al.*, 2002) and grapevine berry (Esteban *et al.*, 1999). In various mango cultivars like 'Nam Dok Mai', 'Langra' or 'Dashehari', it was noted a rise in titratable acidity during the early period of their development followed by a decline till the end of their growth (Mendoza and Wills, 1984; Mukerjee, 1959). It was in agreement with the seasonal pattern of citric acid (first increase, then decrease), the predominant organic acid in mango flesh, observed from 90 days after full bloom. Malic acid shows different changes with various cultivars (Lizada, 1993). However, as in the present study, various results have indicated that malic acid concentration decreases at the beginning of fruit growth and then increases slightly, in particular during ripening (Selvaraj and Kumar, 1994). It was in agreement with a model of malic acid accumulation in peach fruit proposed by Lobit (1999). As the fruit develops, biochemical compounds, like K, are stored in the vacuole, they increase slightly fruit pH which causes a decrease in malic acid concentration. Whereas during the latter stages of fruit development, fruit pH increased (in mango flesh, the pH increased from 3 to 4.5 during fruit growth, data not shown) and had a positive effect on malic acid concentration according to the model.

Carbohydrate metabolism plays an important rule during mango fruit development, particularly changes in starch content (Lakshimnarayana *et al.*, 1970). Fructose and glucose come from sucrose hydrolysis and glucose is also produced by starch hydrolysis. These hexoses are then used for respiration and fruit growth. Fructose represented about 20 to 30 % of total sugars during the fruit development, so it could be considered as a storage sugar in mango. Moreover, because of its higher sweetness than the others sugars, fructose may account a significant part in the sweet taste of mango. As this form of sugar is 1.7 sweeter than sucrose and sucrose was about 20 to 70 % of total sugars, fructose may account for 30 to 70 % of the sweet taste of mango fruit during its growth. From 140 days after full bloom onwards glucose concentration tended to become constant. It was in agreement with studies on reducing sugars during ripening (Hubbard *et al.*, 1991). During this period starch content decreased due to its hydrolysis. In mango, this conversion of insoluble sugar to soluble sugar is enabled by an increase of the activity of starch metabolising enzyme, in particular α-amylase (Jacobi *et al.*, 2002) which was found to be inactive in unripe 'Haden' and 'Kensington' mango fruit (Fuchs *et al.*, 1980). However, the breakdown of starch during later stages of fruit development led mainly to an increase in sucrose concentration rather than to

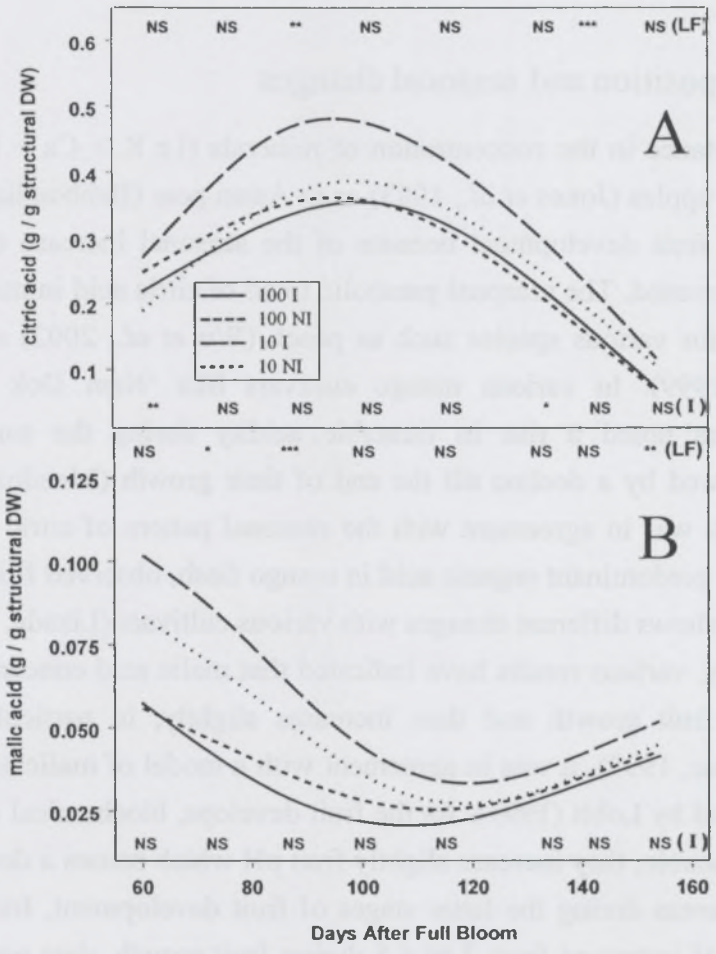

Figure 3: Seasonal variation of citric and malic acid concentrations in g per g of structural dry weight during the 2001 experimental period. The label 10 and 100 indicated the leaf to fruit ratio. I and NI indicate well-irrigated and no irrigated treatments. Differences between the leaf to fruit ratio (LF) or between the irrigation treatment (I) were either significant at $P<0.10$ (*), $P<0.05$ (**) or $P<0.01$(*) or non-significant (NS) on each sampling date. Levels of significance of the difference were shown at the top of each figure (LF) and at the bottom (I). All the curves were smoothed using the 'loess' method (Splus, statistical software, MathSoft Inc., Cambridge, MA).

an increase in glucose. In fact, mango flesh temporarily stored starch from 0.05 g per g of structural dry weight until 1.0 to 1.2 g per g of structural dry weight before it accumulated sucrose from 0.1 g per g of structural dry weight until 1.0 to 1.25 g per g of structural dry weight. Our results indicated that starch was mobilised to provide about 85 % of the carbon required for sucrose accumulation.

2.4.2 Assimilate and water supply affect fruit quality

In the present study, it was shown that increasing the number of leaves per fruit increased mango fruit growth rate and final fruit size at harvest, as reported earlier for other cultivars by Chacko *et al.* (1982) and Reddy and Singh (1991). Fruits from treatment with 100 leaves per fruit were larger than those from treatment with 10, implying that fruit thinning could be advantageous for improving mango fruit size, provided that fruit retention rate is adequate. Mango fruit size was not affected by reducing irrigation under the conditions of this study, that is different from report on irrigation management on 'Kensington' fruit (Diczbalis *et al.*, 1995). Although the irrigation was completely withheld early in the season of fruit growth, deep loamy soil and extensive root system with deep tap roots and rainfall (170 mm during this period) might have presented the trees from experiencing medium to severe water stress under our experimental conditions.

Fruits on branches with a high leaf to fruit ratio had flesh with the greatest total dry matter content. Our earlier studies on water and dry matter accumulation in mango fruits (Léchaudel *et al.*, 2002) have shown that both dry matter and water increase with increasing the leaf to fruit ratio, and the leaf to fruit ratio affected dry matter supply more than water supply. Similar increases in dry matter content with higher leaf to fruit ratio were observed for 'Kensington' mango fruit by Simmons *et al.* (1998). Irrigation treatment seemed to have an effect on total dry matter content of the flesh, for $P<0.10$. The largest difference was for flesh from fruits within treatment with 10 leaves per fruit: those on trees without irrigation had higher total dry matter content. Irrigation effect on total dry matter content of 'Kensigton' mango fruit was also noted by Diczbalis *et al.* (1995). The structural dry matter content of fruit flesh was not affected by treatments. This result implies that the effect of assimilate and water supply on the concentration based on fresh weight of an element x was only due to changes in total dry matter content and in the concentration of non-structural compounds per structural dry weight of the flesh.

Cations were differently affected by leaf to fruit ratio. K concentration was not affected by leaf to fruit ratio. This cation is translocated into fruit with assimilate trough the phloem (Nooden, 1988). Thus, the leaf to fruit ratio possibly influences both the assimilate and K translocation to the fruit in the same way. The results on apple (Volz *et al.*, 1993) and mango (Simmons *et al.*, 1998) which reported that higher leaf to fruit ratio increases fruit K

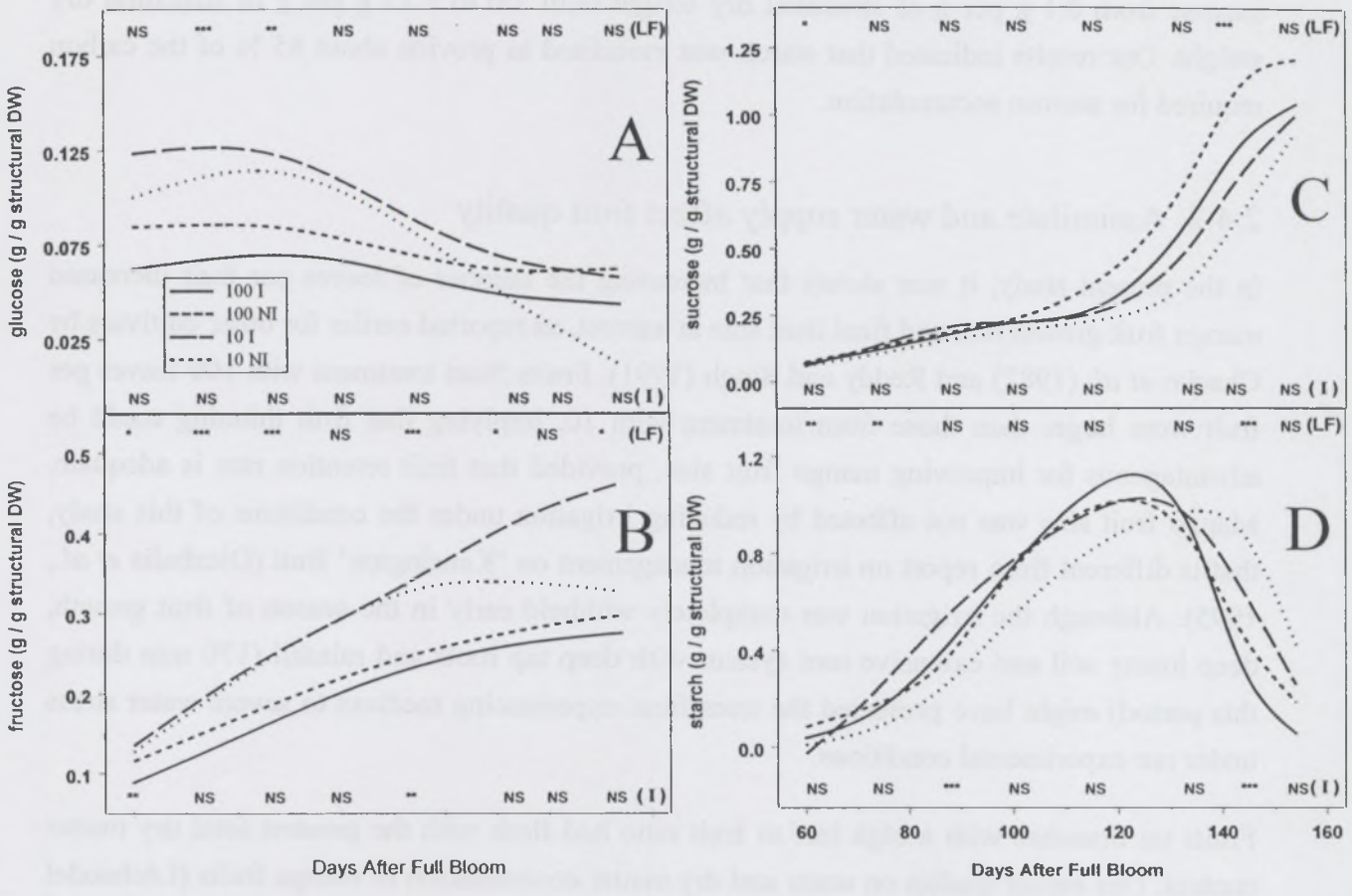

Figure 4: Seasonal variation of glucose, fructose, sucrose, and starch concentrations in g per of structural dry weight during the 2001 experimental period. The label 10 and 100 indicated the leaf to fruit ratio. I and NI indicate well-irrigated and no irrigated treatments. Differences between the leaf to fruit ratio (LF) or between the irrigation treatment (I) were either significant at $P<0.10$ (*), $P<0.05$ (**) or $P<0.01$(*) or non-significant (NS) on each sampling date. Levels of significance of the difference was shown at the top of each figure (LF) and at the bottom (I). All the curves were smoothed using the 'loess' method (Splus, statistical software, MathSoft Inc., Cambridge, MA).

concentration on fresh weight basis possibly reflect difference in total dry matter content of the flesh. The effect on Mg concentration was less marked, but could also be explained in the same way as for K. Results showed that Ca concentration was up to 50 % higher in flesh fruit from treatment with 10 leaves per fruit than from treatment with 100 leaves. Faster fruit growth rate for high leaf to fruit ratio and a decline in surface area:volume ratio as fruit enlarge may reduce water lost per unit of fruit weight via transpiration and the rate of Ca accumulation (Wilkinson, 1968). Moreover, diurnal fluctuations in fruit growth have been linked to bi-directional fluxes in apple fruit (Lang and Volz, 1998). They have found a positive relationship between xylem sap inflows during the night and xylem sap outflows during the day. (Jones *et al.*, 1983) presented evidence that the outflowing sap contains much less Ca than the inflowing sap. Urban *et al.* (2002) showed on mango that decreasing the leaf to fruit ratio from about 100 to about 25 leaves per fruit increased the leaf diffusive conductance to water vapour of about 45 %. Thus, larger amounts of water may be lost during the day by fruits from the low leaf to fruit ratio treatment due to the higher transpiration rates of surrounding leaves. At night, larger quantities of water would enter into these fruit via the xylem replenish water lost during the day, provide also additional import of Ca into the fruit, as well as extra water for fruit growth.

Low assimilate supply increased significantly malic acid concentration, especially early in the season. That was in agreement with a negative relationship found in peach flesh between assimilate supply and malic acid concentration at the beginning of growth (Wu *et al.*, 2002). However, at maturity, malic acid concentration was not positively correlated with assimilate supply as observed in peach. Fruit flesh from treatment with fewer leaves seemed to store more malic acid and cations. Lobit (1999) reported that in ripe fruit malic acid concentration was linked with total cations concentration. Low assimilate supply increased citric acid concentration. Citric acid production takes place in mitochondria and is mainly affected by respiration demand of fruit (Douce, 1985). Citric acid is synthesised when fruit growth is slower and when energetic demand is lower (Lobit, 1999). Thus, fruit flesh from lower leaf to fruit ratio may accumulated more this organic acid.

Glucose concentration was lower in larger fruit. The effect of leaf to fruit ratio in the latter stages of fruit development was less evident. The beginning of starch hydrolysis at these stages could explain this. Higher leaf to fruit ratio tended to decrease fructose concentration. In the case of the shortage of assimilate supply the higher glucose and fructose concentrations may contribute to osmotic adjustment. Higher concentrations of hexoses were found in apple (Wang and Stutte, 1992), mandarin (Yakushiji *et al.*, 1996) and in strawberry (Pomper and Breen, 1997) fruit under water stress. Leaves from the lowest leaf to fruit ratio had higher leaf diffusive conductance to water vapour (Urban *et al.*, 2002) and possibly lower water potentials as Berman and Dejong (1996) found on leaves from trees with heavy crop load. Storage of hexoses in fruit may occur by active accumulation to maintain water inflow in fruit

and a positive cell turgor. This strategy contributes to continued growth during water stress and perhaps during the time of low assimilate supply.

The rates of sucrose accumulation and starch breakdown seemed to be higher when assimilate supply increased, as it was reported on peach fruit (Souty *et al.*, 1999), and to be delayed in fruit flesh from treatment with the lowest assimilate and water supply. It could be explain by a strong relationship between sucrose and the rate of assimilate inflow and by an increase of enzyme activities related to sucrose accumulation. In muskmelon fruit, sucrose phosphate synthase activity was higher in mesocarp from control than in fruits developed with lower leaf area (Hubbard *et al.*, 1990). Near fruit maturity, the different levels of sucrose and starch concentrations among treatments may provided consequences on the quality of these fruits, in particular concerning their taste.

As far as fruit quality is concerned, element concentrations expressed per structural dry weight of flesh give more information on what quality components were affected by water and assimilate supply all along fruit development. Firstly, higher assimilate supply increased total dry matter content of mango fruit flesh. Secondly, the part of structural material seemed to be similar regardless treatments. Finally, seasonal changes of composition of the non-structural compounds were mainly affected by assimilate supply and less by irrigation treatments. Less assimilate supply tended to increase Ca, malic and citric acid concentrations. Others cations, such as Mg and K, were less affected by leaf to fruit ratio. Sucrose concentration was increased by higher assimilate supply. Near maturity the eating quality of fruit seemed to be improved by higher leaf to fruit ratio as those fruits contained more sucrose, less starch and acids, which increased the sweet taste. However it appeared that fruit's shelf life might be affected, as concentration of Ca expressed by structural dry weight was lower.

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Chapitre III : Étude du fonctionnement carboné de la mangue : Combined effects of climate and source / sink relations on mango fruit growth studied by a modelling approach

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L'accumulation de matière sèche dans le fruit est sous l'influence de la disponibilité en assimilats carbonés, facteur principal qui peut varier au sein d'un arbre. Nous faisons donc l'hypothèse que le rapport feuilles/fruit influence la croissance en matière sèche du fruit en modifiant les relations sources/puits à l'échelle du rameau qui affectent alors les processus physiologiques impliqués dans la croissance en matière sèche, comme la photosynthèse foliaire, les respirations d'entretien et de croissance, l'évolution des réserves dans les feuilles et le bois, ou la demande du fruit.

Dans l'objectif de comprendre le fonctionnement carboné de la mangue, la croissance en matière sèche de ce fruit a été étudiée puis modélisée au niveau d'un rameau qui comprend des feuilles assimilatrices de carbone, du bois et des fruits en croissance. Un modèle a été adapté pour reproduire le fonctionnement carboné du rameau fructifère en prenant en compte les variations des relations sources/puits selon les conditions environnementales (Léchaudel, M., Génard, M., Urban, L. and Jannoyer, M. Combined effects of climate and source / sink relations on mango fruit growth studied by a modelling approach. Manuscript qui va être soumis à *Tree Physiology*). Des hypothèses sont proposées pour reproduire l'effet de ces variations sur les processus physiologiques intégrés dans le modèle. Les sorties du modèle sont ensuite comparées aux mesures, et le modèle est utilisé dans une étude virtuelle pour quantifier la contribution du climat et des principaux facteurs de variations des relations sources/puits dans les processus impliqués dans la croissance en matière sèche du fruit.

Combined effects of climate and source / sink relations on mango fruit growth studied by a modelling approach

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ABSTRACT

To assess the respective contribution of climate changes, initial fruit dry mass and leaf-to-fruit ratio on processes involved in sources/sink balances and fruit growth, leaf photosynthesis, fruit demand, respiration, and reserves mobilisation in leaves and stem, were characterised at the shoot bearing level on mango. Fruit dry mass was measured during three successive years, on various leaf-to-fruit ratio treatments. From these results a model of fruit growth was developed for mango fruit. This model is able to account accurately for the variations of the main processes involved in fruit growth, as the decrease of leaf photosynthesis and the high reserves content in leaves and stem observed for high leaf to fruit ratio treatments. Simulation results during the three successive years and for the various leaf-to-fruit ratio treatments showed a good agreement with the observed data of fruit growth. The initial fruit dry mass introduced to compute the maximum fruit dry mass in the fruit demand expression, allowed to represent sink size in the early stage of fruit development assumed to be proportional to cell number and thus to account climatic and resource limitations which may affect cell division and fruit growth. Moreover, simulations on fruit growth assessed with various climate conditions and different source/sink factors (initial fruit dry mass and leaf-to-fruit ratio) demonstrate that variations in fruit growth between years can be partly explained by climate variations through their effects on leaf photosynthesis, fruit demand, and fruit growth rate. However, climate changes contribute less to observed changes in fruit growth than the initial fruit dry mass and the leaf-to-fruit ratio.

1 Introduction

Fruit dry mass is an important ingredient of fruit quality, since dry matter covers mainly carbohydrates, 60 % of which are sugars and acids, the main compounds involved in fruit taste (Fishman and Génard, 1998; Mukerjee, 1959). Carbohydrates are synthesised by leaf photosynthesis, then supplied via the phloem to the sinks, among which fruits take a large part in the case of fruit trees.

The amount of carbohydrates produced by photosynthesis is related to the leaf area and to the photosynthetic capacity and activity. The latter can be influenced by climatic conditions (Le Roux *et al.*, 2001; Rosati *et al.*, 1999) and by changes in sources/sink balances, as it has been reported in many species, including apple (Palmer, 1992), grapevine (Naor *et al.*, 1997), and mango (Urban *et al.*, 2003). Factors affecting leaf photosynthesis generally modify carbohydrate content in leaves (Foyer, 1988). This accumulation/depletion of carbohydrates in the source leaves is generally believed to be the result of the balance between sink demand and photosynthetic rates (Ben Mimoun *et al.*, 1996).

The sink demand is generally defined as the sum of the assimilates required for maintenance and potential growth of the sink organ, the latter being determined under optimal environmental conditions, i.e. non-limiting supply of carbon and other resources (Ho, 1992; Warren Wilson, 1972). The potential growth of fruit is related to fruit mass, i.e. sink size, and to the relative fruit growth rate, i.e. sink activity, both determining sink strength which is in fruits the ability to attract assimilates to sustain fruit growth.

Many cultural practices, by manipulating either source size or sink size, influence source-sinks relationships involved in fruit growth. Thinning, which generally consists in removing the smallest fruits, affects sink size. This technique, which aims at controlling crop load, is known to usually increase fruit size sometimes at the expend of yield (Goffinet *et al.*, 1995). Pruning or partial defoliation is another practice which decreases total leaf area, and thus source size (Layne and Flore, 1993). Girdling is known to favour carbohydrate accumulation and fruit size, while reducing shoot growth (Cutting and Lyne, 1993).

Variation in fruit growth from year to year is sometimes observed, and may be caused by climatic changes from one season to another. Light is required for photosynthesis and

increased light levels could improve fruit size in the case of mango (Mendoza and Wills, 1984), pear (Kappel and Neilsen, 1994), and apple (Morgan *et al.*, 1984), according to the fruit demand limitation. Fruit growth depends upon physiological and biochemical processes, which are under the influence of the temperature prevailing during the development period. Temperature was found to be a source of variation of fruit growth rate in several fruit species, such as apples (Tukey, 1960), satsuma mandarin (Marsh *et al.*, 1999) and peach (Haun and Coston, 1983). It appears in many studies that cumulative degree day after full bloom is an adequate variable to explain the variability of growth between years and local sites (Burondkar *et al.*, 2000; Mosqueda-Vasquez and Ireta-Ojeda, 1993).

Modelling the distribution of carbohydrates within individual fruit trees is important to predict the fruit growth (Grossman and Dejong, 1994; Lescourret *et al.*, 1998). Models of fruit growth in dry mass have been successfully used to determine the yield of horticultural fruit crops (Marcelis *et al.*, 1998) and to identify environmental factors limiting fruit growth (Génard *et al.*, 1998; Grossman and Dejong, 1994). In fruit trees, the variability of fruit growth is generally large within the plant and models have to focuse on important production units such as shoots bearing fruits. At this level the major physiological processes involved in fruit growth can be studied through a model. The model of (Lescourret *et al.*, 1998) is able to take into account source/sink relationships and this possible variation in growth of the girdled shoot bearing fruit through simulating main processes, as source activity, reserves mobilisation, respiration, and fruit demand.

Mango fruit is an important tropical horticultural crop and is generally noted to have a strong heterogeneity of fruit size at harvest. The objective of this study is to quantify the respective effects of climate, early sink size and leaf-to-fruit ratio, and their interactions on fruit growth and fruit size at harvest. In a first step, an approach coupling field experimentations and modelling mango fruit growth was developed at the girdled shoot bearing fruit level to analyse the source/sink relationships in mango. The source activity, the sink demand, the respiration of the various organs and the reserves mobilisation were characterised. The capacity of the model to account for the differences in fruit dry mass between various leaf-to-fruit ratio treatments was tested. The sensitivity of fruit growth to the model parameters was studied. In a second step, the combined effects of climate and source/sink factors (leaf-to-fruit ratio, initial fruit dry mass) were studied using the model. With such a kind of simulations, it is possible to vary factors exactly as expected while maintaining the other traits of the system similar between treatments. This part of our study requires to have an important set of climate data from various years and sites, and a model beforehand capable to predict fruit growth at various source/sink ratios with good accuracy during several years.

2 Materials and methods

2.1 Plant material

The experimental study was conducted on 11-year-old (in 2000) mango trees of cv. 'Lirfa', grafted on 'Maison Rouge', in La Réunion island (20°52'48''S, 55°31'48''E) during the 2000, 2001 and 2002 growing seasons. The 2000 experimental plot, on orchard 1, consisted of ten rows, 7 m distant, each of them made of nine trees spaced 5 m apart, and about 3 m high. The trees observed in 2001 were spaced 5 m by 6 m and were around 3 m high in an adjacent plot, called orchard 2. In 2002, experimental data were acquired from the two orchards.

During the experiment, all trees were irrigated every two days at 100 % replacement of evaporation. Six weeks after flowering, about ten to fifteen branches per tree were chosen, which represents less than 10 % of the total branches of the tree canopy. The branches were all chosen on the top of the canopies to reduce the variability of light received by leaves which could significantly change carbon assimilation and fruit growth as well. Branches were girdled by removing a band of bark 10-15 mm wide. They were sometimes defruited and defoliated if needed to reach 10, 25, 50, 100 and 150 leaves per fruit (with 50 leaves for 5 fruits, 100 leaves for 4, 2 and 1 fruit, and 150 leaves for 1 fruit, respectively). To keep the leaf-to-fruit ratio constant within each treatment, new emerging leaves were removed. Girdling was performed after the heavy young fruit drop, when fruit length was about 5 cm.

2.2 Model Presentation

The model of carbon partitioning at the shoot-bearing fruit level proposed for peach by Lescourret *et al.* (1998) was modified to take into account mango fruit properties. This model describes the functioning of a system composed by three main components: fruit, leaves, and stem. The vegetative part is of the current or the previous year. Carbohydrates partitioning is simulated, based on organ demand and priority rules. Mango leaves and girdled stem do not grow during the fruit growing season. The priority rules are: 1) maintenance of the system, 2) reproductive growth, and 3) accumulation of reserves in the leaves and then in the stem. When the potential fruit demand is higher than carbohydrates supplied by current photosynthesis, the fruit can obtain assimilates from the stem and leaf reserves. Organ respiration and reserve mobilisation are represented as in the initial model of Lescourret *et al.* (1998). New equations are proposed for carbon assimilation and fruit demand. Parameters of

Table 1: Symbols, units, and definitions of model parameters for mango

Parameter	Equation	Value	Significance
Carbon assimilation by leaves			
p_1 (µmol CO_2 m^{-2} s^{-1} g^{-1})	Eq. 1	3.85 ± 0.57	Initial slope of the response curve of light-saturated photosynthesis to fruit demand
p_2 (µmol CO_2 m^{-2} s^{-1})	Eq. 1	33.23 ± 11.91	Light-saturated maximal leaf photosynthesis
p_3 (dimensionless)	Eq. 1 (Appendix 2)	0.483 ± 0.074	Parameters of the response of leaf photosynthesis to radiation and light-saturated photosynthesis
p_4 (dimensionless)	Eq. 1 (Appendix 2)	0.034 ± 0.007	
Maintenance respiration			
MRR_{leaves} (g carbon g^{-1} $hour^{-1}$)	Eq. 3 (Appendix 2)	$1.56\ 10^{-4}$	Maintenance respiration rate of leaves, stem, and fruit components
MRR_{stem} (g carbon g^{-1} day^{-1})	Eq. 3 (Appendix 2)	$8.58\ 10^{-4}$	
MRR_{fruit} (g carbon g^{-1} day^{-1})	Eq. 4	$1.15\ 10^{-3} \pm 1.1\ 10^{-4}$	
Q_{10}^{leaves} (dimensionless)	Eq. 3 (Appendix 2)	2.11	Q_{10} value for leaves, stem, and fruit components
Q_{10}^{stem} (dimensionless)	Eq. 3 (Appendix 2)	1.96	
Q_{10}^{fruit} (dimensionless)	Eq. 3 (Appendix 2)	1.90	
Fruit growth			
RGR_{ini} (dd-1)	Eq. 2	0.0105 ± 0.0003	Initial relative growth rate
a (dimensionless)	Eq. 3	16.736 ± 1.637	Parameters for computing the maximum fruit dry mass from the initial fruit dry mass
b (dimensionless)	Eq. 3	0.624 ± 0.036	
GRC_{fruit} (g carbon g^{-1})	Eq. 4 and 5	0.04 ± 0.01	Growth respiration coefficient of fruit
c_{fruit} (g carbon g^{-1})	Eq. 5	0.4239 ± 0.0048	Carbon content of fruit
Reserve mobilisation			
r_4	Eq. 5 (Appendix 2)	0.0162	Mobile fraction of reserves in leaves
r_5	Eq. 6 (Appendix 2)	0.0164	Mobile fraction of reserves in stem

the fruit growth and maintenance respiration, and reserves mobilisation in the stem and the leaves were established from experiments in mango cv. Lirfa (see 'Measurements for parameters assessment'). A schematic representation of the model is proposed in Appendix 1.

A list of the model parameters is presented in Table 1.

2.2.1 Carbon assimilation by leaves

For many plant species it has been noted that a balance is maintained between source supply and sink demand (Foyer *et al.*, 1995; Fujii and Kennedy, 1985; Ho, 1992). In grapevines, measurements suggest that photosynthesis is regulated by an internal factor, possibly related to sink demand (Quereix *et al.*, 2001). Such results are well described by a model based on the assumption that phloem-based feedback signal regulates the balance between source and sink activities (Quereix *et al.*, 2001). To take into account the effect of fruit demand on photosynthesis, we adapted the simple model proposed by Ben Mimoun *et al.* (1996), which assumes that the light-saturated leaf photosynthesis P_{max} (µmol CO_2 m^{-2} s^{-1}) is an asymptotic function of fruit demand, D_{fruit} (g C m^{-2} d^{-1}):

$$P_{max} = \frac{p_1 * D_{fruit} * p_2}{p_1 * D_{fruit} + p_2} \quad if \; P_{max} < P^*_{max}$$
$$P_{max} = P^*_{max} \quad if \; P_{max} \geq P^*_{max} \qquad (1)$$

with p_1 (µmol CO_2 m^{-2} s^{-1} g C^{-1}) represents the initial slope of the response curve of P_{max} to D_{fruit}, p_2 (µmol CO_2 m^{-2} s^{-1}) a parameter and P^*_{max} (µmol CO_2 m^{-2} s^{-1}), the potential light-saturated photosynthesis which is equal to 15, the maximal value obtained from all our measurements of leaf photosynthesis.

To calculate photosynthesis per unit leaf area and per unit time (µmol CO_2 m^{-2} s^{-1}), we used the same formulation (Appendix 2, equation 1) than in the model of Lescourret *et al.* (1998). The net photosynthesis is a function of the light-saturated leaf photosynthesis, calculated in equation 1, the photosynthetically active flux density, PPFD (input data, in µmol photon m^{-2} s^{-1}), and two parameters, p_3 and p_4 estimated experimentally (Appendix 2, equation 1). The net photosynthesis of shaded leaves is calculated from the radiation received by those leaves which is obtained by an empirical relationship with PPFD, named g(PPFD), defined on an experimental basis.

The fraction of sunlit and shaded leaf area is estimated from experimental measurements taken by fish-eye photographs and considering that shadow changes during the day according to the course of the sun, as explained by Lescourret *et al.* (1998).The amount of carbon

produced by leaf photosynthesis during a day is considered as the sum of hourly photosynthesis of the sunlit leaf area and of the shaded leaf area (Appendix 2, equation 2), as proposed in the model of Lescourret *et al.* (1998).

2.2.2 Fruit demand

The fruit demand is function of the potential fruit growth, the carbon concentration in the fruit, and the growth respiration coefficient (Appendix 2, equation 4), as in Lescourret *et al.* (1998). The potential growth of mango fruit was computed by a logistic equation. A link between the maximal fruit dry mass and the fruit dry mass at the early stage of development was introduced. The potential fruit growth or sink strength is generally described as the product of sink size by sink activity. The potential fruit growth, attained when the fruit is grown under optimal environmental conditions in the presence of a non-limiting supply of carbon and other resources, in our case under 100 or 150 leaves per fruit, could be easily represented as:

$$\frac{\Delta DM_f^{pot}}{\Delta dd} = RGR_f^{ini} * DM_f * \left(1 - \frac{DM_f}{DM_f^{max}}\right) \quad (2)$$

with Δdd, the daily variation of degree days (dd), RGR_f^{ini}, the initial relative fruit growth rate (dd^{-1}), DM_f, the fruit dry mass (g), i.e. the sink size, and DM_f^{max}, the maximal final dry mass (g).

The maximal final mass of fruit depends generally on the final number of cells in the fruit, as demonstrated by several authors on many species, as apple (Goffinet *et al.*, 1995), peach (Scorza *et al.*, 1991), tomato (Bertin *et al.*, 2002), and apricot (Jackson and Coombe, 1966). This relationship was also observed in previous studies on mango fruit (data not shown). For mango, cell division in the flesh occurs until 35 to 45 days after full bloom in commercial cultivars (Saini *et al.*, 1971). As the number of cells is not always easy to measure, we proposed a simple relationship between the maximal final mass and an 'initial' fruit mass, assumed to be proportional to cell number, i.e. at about 350 degree days, which corresponds to 60 to 70 days after full bloom when cell division phase is finished:

$$DM_f^{max} = a * \left(DM_f^{ini}\right)^b \quad (3)$$

with DM_f^{ini}, the initial fruit dry mass at about 350 degree days, a and b parameters.

2.3 Measurements of fruit growth

Two kinds of fruit growth measurement were made: either the same fruit was monitored (diameter measurement) along the growing season, or the fruit was harvested, weighed and its diameter measured at a given date ('destructive' measurement in this case). During the first flowering of the 2000 growing season, six fruits from five leaf-to-fruit ratios (10, 25, 50, 100, and 150 leaves per fruit) were harvested each week between 15 November 2000 and 4 January 2001. The same year, the diameter of eight fruits, originated from the first flowering, and the diameter of eight other fruits, from the second flowering, were measured every week between 29 October 2000 and 20 December 2000 and between 11 December 2000 and 7 February 2001, respectively. Five leaf-to-fruit ratios were applied: 10, 25, 50, 100, and 150 leaves per fruit for the first flowering, and 10, 25, 50, 75, and 100 for the second one. In 2001, there was only one flowering flush. Six fruits from two leaf-to-fruit ratio treatments (10 and 100 leaves per fruit) were harvested every fifteen days between 19 October 2001 and 21 January 2002. During the 2002 growing season, the diameter of ten fruits grown under 100 leaves per fruit treatment was measured for the two flowering episodes in orchard 2, and for the first one in orchard 1. The data of harvested fruits in 2001 were used to convert the diameter of each fruit in dry mass by an allometric relationship. For each harvested fruit, the fruit fresh mass was measured. A sample of each component was taken from each fruit, weighted, and then dried at 75°C for 48 h, and the corresponding dry masses recorded.

2.4 Measurements for parameters assessment

2.4.1 Growth and maintenance respiration of fruit

Coefficients of growth and maintenance respiration of mango fruit are needed.

The growth respiration coefficient was deduced from construction costs measurements.

The total nitrogen and carbon concentration (g g^{-1} dry mass) of each fruit sample was measured on 5 mg of plant material powder using an automated CN analyser (Carlo Erba analyzer ANA1500, Thermo Finnigan, Les Ulis, France) according to the ANCA-MS technique. Ash content was determined after combustion of 1 g aliquot for 12 hours in a muffle furnace at 420°C and weighing of the remaining residue.

The construction costs, CC (g glucose g^{-1}), was calculated as a function of the concentrations (g g^{-1} dry mass) of fruit tissue in carbon (C), nitrogen (N) and ash (ASH), and the energetic costs of nitrogen assimilation and carbohydrate translocation (Vertregt and Penning de Vries, 1987; Wullschleger *et al.*, 1997):

$$CC = \left(5.39 \cdot C + 0.80 \cdot ASH + 5.64 \cdot f_{N,h} \cdot N - 1.191\right) \cdot \left(1 + r_T\right)$$

where $f_{N,h}$, represents the fraction of nitrogen used in growth that is assimilated heterotrophically, assumed to be equal to 1 for fruit (Wullschleger *et al.*, 1997), r_T, the added cost of translocating photosynthetates from sources to sinks, equal to 5.3 % (Vertregt and Penning de Vries, 1987).

The coefficient GRC_{fruit} must be expressed on a g of carbon per g of dry mass basis in the model. To derive it from the *CC* value, the two following equations are needed:

$$\frac{d(DM)}{dt} \cdot (CC \cdot \alpha) = G_{assim} \tag{4}$$

$$\text{and} \left[\frac{d(DM)}{dt} \cdot c_{fruit}\right] + R_g = G_{assim} \tag{5}$$

with *d(DM)/dt*, the rate of dry mass increase of the fruit (g day^{-1}), G_{assim}, the net gain of assimilates in the fruit (g C), α, the concentration of carbon in glucose ($\alpha = 0.4$), c_{fruit}, the carbon content of the fruit, and R_g, the fruit growth respiration (g C day^{-1}).

We derived the coefficient of growth respiration by combining equations 4 and 5:

$$R_g = \left(CC \cdot \alpha - c_{fruit}\right) \cdot \frac{d(DM)}{dt} \text{ with } GRC_{fruit} = CC \cdot \alpha - c_{fruit} \tag{6}$$

In 2002, total fruit respiration was collected by gas exchange measurements on fruit during four different days in the growing season. On each measurement day, three fruits from each treatment, i.e. 10 and 100 leaves per fruit, were harvested, weighted, and then placed within a closed chamber. Carbon dioxide production was determined by gas chromatography (Agilent M200). A poropak type B was used isothermally at 60°C. The gas carrier was helium.

The total respiration rate per fruit (R in g C day^{-1}) was described to take into account maintenance and growth respiration (Thornley, 1970):

$$R = MRR_{fruit} \cdot DM + GRC_{fruit} \cdot \frac{d(DM)}{dt} \tag{7}$$

where *DM* is the fruit dry mass (g), *dW/dt* the fruit growth rate (g day^{-1}), and MRR_{fruit} and GRC_{fruit} represent the coefficients for maintenance (g C g^{-1} day^{-1}) and growth (g C g^{-1}) respiration. The coefficient of maintenance respiration (MRR_{fruit} in g g^{-1} day^{-1}) was estimated using equation 7, from measurements of total fruit respiration, fruit dry mass, obtained after a conversion of the fruit fresh mass into fruit dry mass using an allometric relationship, fruit

growth rate in dry mass derived from fruit dry mass, and using the estimated coefficient of growth respiration.

2.4.2 Light saturated photosynthesis

Leaf gas exchanges were measured with an infrared gas analyser and a leaf chamber system with a red+blue light source (LI 6400, Li-Cor Inc., Lincoln, USA). Calculations were performed according to von Caemmerer and Farquhar (1981). Measurements were performed at C_a = 36 Pa in the tracking mode (to minimise light fluctuations) on well-exposed, young fully expanded leaves from three leaf to fruit ratio treatments (25, 50, and 100 leaves per fruit). Measurements were performed on 7 selected days from 15 November 2000 to 4 January 2001.

Parameters of the response of the net photosynthesis to PPFD, p_3 and p_4, were estimated regardless of the leaf-to-fruit ratio, using the whole set of leaf gas exchange data.

The function g(PPFD) representing the radiation received by the shade leaves was assessed with measurements of radiation received by a shade leaf ($PPFD_{shaded}$) and measurements few time after of radiation received by a sunlit leaf ($PPFD_{sunlit}$), using the radiation sensor of Li-Cor.

The light-saturated leaf photosynthesis was deduced from gas exchange data, by retaining net photosynthetic assimilation measured when the photosynthetically active flux density (PPFD) was higher than 1300 µmol photon m^{-2} s^{-1}. Parameters p_1 and p_2 of equation 1 were estimated from data set of light-saturated photosynthesis performed on leaves from treatments 25, 50, and 100 leaves per fruit in 2000 growing season, and fruit demand measured on fruits carried on the same shoot, calculated from their growth rate, dry mass, and carbon content.

2.4.3 Potential fruit growth and base temperature

Parameters of potential fruit growth, RGR_f^{ini}, a and b (to calculate DM_f^{max}, the limiting final mass), as described in equations 2 and 3, were estimated by using observed data of seasonal variation of fruit growth, from treatment 100 and 150 leaves per fruit during the 2000 growing season, and 100 leaves per fruit during the 2001 and 2002 growing seasons.

The daily variation of degree days (Δdd), used in equation 2 to assess potential fruit growth, DM_f^{pot}, is computed with maximum and minimum daily temperatures recorded, and with lower and upper temperature thresholds (Baskerville and Emin, 1969). Growth and development of tropical plants occurs often between 10°C and 40°C (Mosqueda-Vasquez and Ireta-Ojeda, 1993). The upper temperature threshold was fixed at 40°C. We chose to estimate

the base temperature (T_b) for mango fruit development in La Réunion. The base temperature and the parameters of the potential fruit growth were estimated by minimising the following basic criterion:

$$\sum_k \sum_j \frac{1}{N_j} \sum_i \left(DM^c_{kji} - DM_{kji}\right)^2$$

where k is the data set, N_j is the number of fruit measured for a data set, DM^c_{kji} and DM_{kji} the dry mass of fruit i, calculated by Equations 2 and 3 and measured, respectively, at the date j and the data set k.

2.4.4 Reserves mobilisation

Parameters of reserves mobilisation, r_4 for the mobile fraction of reserves in the leaves, and r_5 for the mobile fraction of reserves in the stem, were assessed by calibration of the model. This 'calibration procedure' used the reserve data collected from 15 November 2000 to 4 January 2001, on 7 selected days for leaves and 4 selected days for stem. Each day of measurements, leaf areas and fresh masses of the different components (stem and leaves) were measured. A sample of each component was taken, weighted, then dried by freeze-drying and the corresponding dry masses recorded. Then, these samples were put at -20°C for future biochemical analysis of reserves. On leaf and stem samples, reserve content was studied by measuring glucose, fructose and sucrose concentrations by HPLC following the method of (Gomez *et al.*, 2002). Starch was determined by enzymatic hydrolysis to glucose (Gomez *et al.*, 2003).

The criterion to be minimised during model calibration was the following it takes into account the reserve content of both leaves and stem:

$$\sum_{k=1}^{3} \frac{1}{{\sigma_{sr_k}}^2} \cdot \frac{1}{N_{sr_k}} \sum_i n_{ki} \cdot \left(sr^c_{ki} - \overline{sr_{ki}}\right)^2 + \frac{1}{{\sigma_{lr_k}}^2} \cdot \frac{1}{N_{lr_k}} \sum_i n_{ki} \cdot \left(lr^c_{ki} - \overline{lr_{ki}}\right)^2$$

where k refers to the leaf-to-fruit ratio treatment (25, 50, and 100 leaves per fruit), labels *sr* and *lr* to the reserve contents (g g^{-1} dry mass) in stem and leaves, respectively, σ^2 are variances of observed data, N is the number of measurement dates for each treatment, n_{ki} the number of measurements at date i and for treatment k, xr^c_{ki} the carbon reserve content at date i for treatment k calculated by the model, and $\overline{xr_{ki}}$ the corresponding average of n_{ki} measurements, with $x=s$ for stem and $x=l$ for leaves.

2.4.5 Allometric relationships

The total leaf area, LA (m^2), was empirically calculated from the number of leaves, n_{leaves}, as $LA = 0.0051 * (n_{leaves})^{0.937}$ ($R^2 = 0.94$, n = 50).

The dry mass (DM) of the fruit was related to the fruit diameter (D) by the empirical relationships ($DM = 0.8736 \cdot e^{(0.0527 \cdot D)}$, $R^2 = 0.91$, n = 210).

2.4.6 Parameters taken from the literature

The values of maintenance respiration rates of stem, MRR_{stem}, and leaves, MRR_{leaves}, at 20 °C, and the respective Q_{10} values were those used by Grossman and Dejong (1994) for peach. The Q_{10} value for fruit respiration maintenance was the one proposed by Dejong *et al.* (1987) for peach fruit.

2.5 Model evaluation

A basic criterion , the root mean squared error (RMSE), describing the mean distance between simulation and measurement (Kobayashi and Us Salam, 2000) was used to evaluate (i) the goodness of fit of the model for data for parameter estimation (quality of adjustment), and (ii) the predictive quality of the model on independent data. This criterion was expressed as:

$$\sqrt{\frac{\sum_{i=1}^{N} n_i \cdot \left(DM_i^c - \overline{DM_i}\right)^2}{\sum_{i=1}^{N} n_i}}$$

with DM_i^c the fruit dry mass at the date i simulated by the model and $\overline{DM_i}$ the average of dry mass measured at the date i for n_i fruits. A relative RMSE, RRMSE, was also calculated as the ratio between the RMSE and the mean of all measurements.

2.6 Modelling Technique

Simulation of seasonal dry mass of the fruit was based on a daily scale, except for photosynthesis, which runs on a hourly basis. The model was written using the S-Plus language (Insightful Corp., USA).

Parameters of regulation of light-saturated photosynthesis, p_1 and p_2, and parameters of the response of net photosynthesis to PPFD, p_3 and p_4, were estimated by nonlinear least squares regression. The parameter of the function of radiation received by shaded leaves (g(PPFD)), k,

and the parameter of maintenance respiration, MRR_{fruit}, were estimated by linear regression. Criteria to estimate parameters of reserve mobilisation, r_4 and r_5, base temperature, T_b, parameters of potential fruit growth RGR_f^{ini}, a and b, were minimised by non-linear adjustment.

2.7 Description of input data

The climatic data were collected by the meteorological station situated close to the orchard. The maximum and minimum daily temperatures were used to compute the sum of growing degree days after full bloom. The hourly global radiation was recorded to simulate leaf photosynthesis. The daily mean temperature was used to calculate maintenance respiration of the various organs.

2.8 Initial conditions

Initial values required by the model for fruit dry mass were chosen equal, for each year, and for each leaf-to-fruit ratio treatment, to the mean of data assessed the first day of dry mass measurement. Initial values for the ratio between reserve mass and dry mass in leaves and stem were obtained from the first day of reserves measurement in 2000. Those values are required for calculating the initial mass of reserves in leaves and stem.

2.9 Description of a simulations used to assess the contribution of climate, initial fruit dry mass, and leaf-to-fruit ratio on fruit growth and underlying physiological processes

The model was run for 14 climatic situations corresponding to seven growing seasons between 1996 and 2002, and for two experimental sites, one in the North-West of the island and the other in the South-West. Two levels of leaf-to-fruit ratios and of initial fruit dry masses were considered. The levels were 50 and 100 leaves per fruit for the leaf-to-fruit ratio, which is consistent with current horticultural practices. For the initial fruit dry mass, a low and a high level, 7 and 21g respectively, were established in order to represent, 0.5 and 2 times the mean fruit dry mass measured in our experiments and allow to represent nearly the variability of measurements. For each climatic situation, the model was run by combining factor conditions. As temperature strongly influences rates of fruit growth and maturation, temperature sum (degree days) is often used as an index of 'physiological time'. In our experiments, during three successive years, and for various leaf-to-fruit ratios, the average of

harvest date for mango was about 1100 degree days after full bloom. At this stage, biochemical analysis showed that starch had decreased and sucrose had increased strongly, respectively. Indicators of fruit quality as the total soluble solids and the flesh dry matter content were higher than 15° Brix and 16 %, respectively (data not shown). This sum of degree days, which was in agreement with the calculated heat units required for other mango cultivars, like 'Carabao', to reach maturity (Mendoza and Wills, 1984),was the stop of fruit growth. The model run until this date.

Different daily variables concerning source and sink functioning were monitored, i.e. photosynthesis and reserves mobilisation in the stem and the leaves, and maintenance and growth respiration, demand and growth rate of the fruit. The mean value of those variables was analysed by analysis of variance (fixed effects). The analysis of variance carried out the main effects and the first-order interactions of the three factors, i.e. climate, leaf-to-fruit ratio, and initial fruit dry mass. The contribution of the different factors and interactions to the variance of the studied variables was calculated as the ratio of the corresponding sum of squares to the total sum of squares.

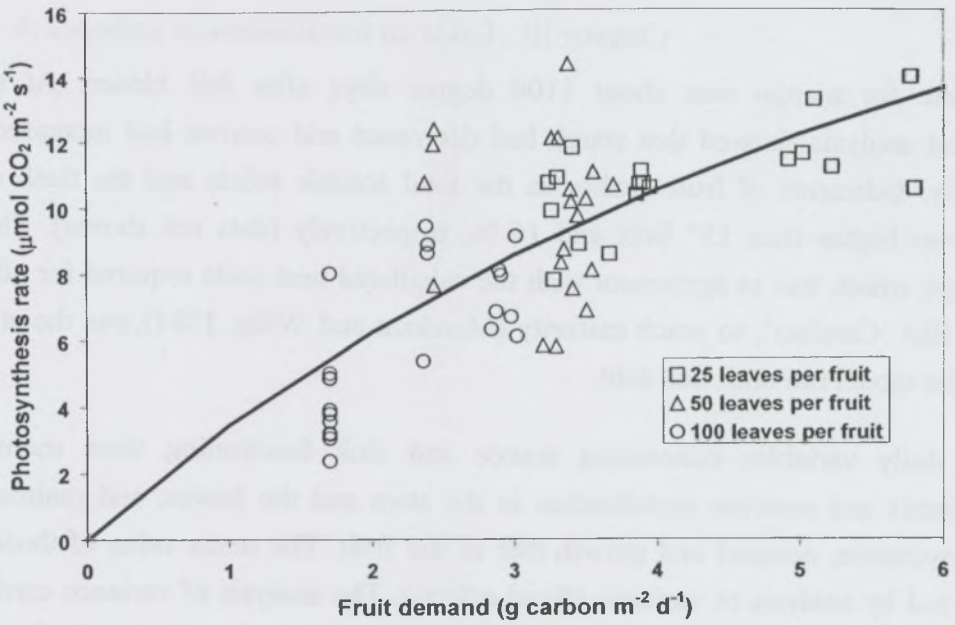

Figure 1: Light-saturated photosynthesis (µmol CO_2 m^{-2} s^{-1}) as a function of fruit demand (g C m^{-2} d^{-1}) for the three leaf-to-fruit ratio treatments, 25 (□), 50 (Δ), and 100 (O). Symbols and the solid line represent measured values and the model fitted to experimental data, respectively.

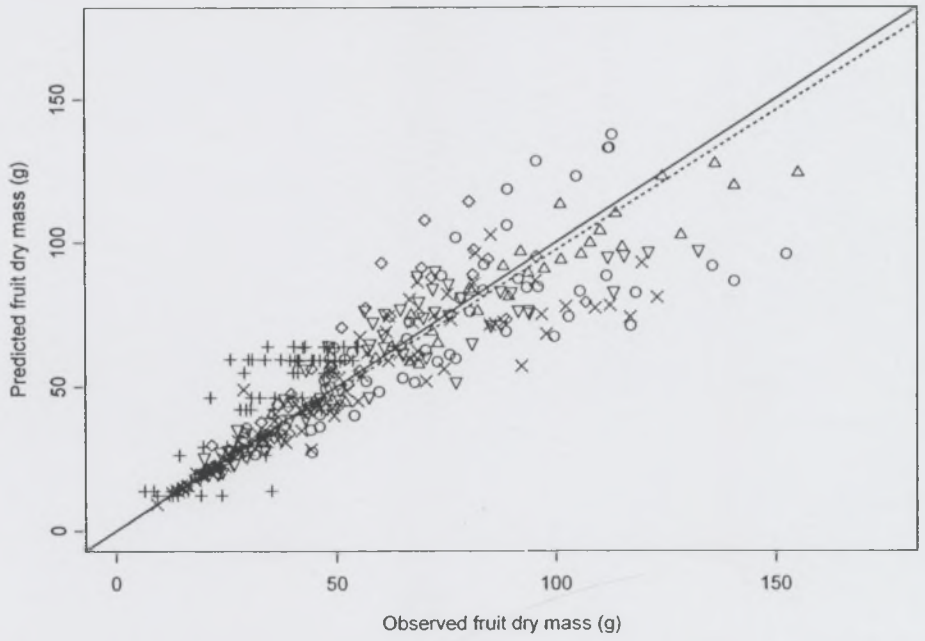

Figure 2: Predicted values of fruit dry mass calculated using the model of potential fruit growth (equation 2), plotted against corresponding observed values. Fruit growth was assessed for data set in 2000 (treatments 100 (O) and 150 leaves per fruit (Δ) originated from the first flowering), for data set in 2001 (treatment 100 leaves per fruit (+)), and for data set in 2002 (treatment 100 leaves per fruit, originated from the first flowering in orchard 1 (×) and 2 (◊) and from the second flowering in orchard 2 (▽)).

3 Results

3.1 Estimation of model parameters

The construction costs, *CC*, measured from biochemical analysis, during the 2000 season on fruits from treatments 25, 50, and 100 leaves per fruit, were 1.11 ± 0.030 g glucose g^{-1} (n = 69) for the fruit, 1.19 ± 0.07 g glucose g^{-1} (n = 69) for the peel, 1.06 ± 0.03 g glucose g^{-1} (n = 69) for the pulp and 1.23 ± 0.04 g glucose g^{-1} (n = 69) for the stone, respectively. The construction costs measured on mango were similar to those estimated in grapevine berries (from 1.1 to 1.4 g glucose g^{-1}; (Vivin *et al.*, 2003)), and in tomato fruit (from 1.15 to 1.24 g glucose g^{-1}; (Gary *et al.*, 1998)). For the flesh component, construction costs were close to those estimated for flesh of cantaloupe (Valantin *et al.*, 1999), whereas those estimated for seeds of cantaloupe were higher than those for stone of mango. The estimated coefficient of growth respiration deduced for these fruits was GRC_{fruit} = 0.04 ± 0.01 g C g^{-1} (n = 69). This fruit growth respiration coefficient was in the same range of coefficients observed for tomato (Penning de Vries *et al.*, 1989), peach (Dejong and Goudriaan, 1989), and cucumber (Marcelis and Baan Hofman-Eijer, 1995), which are 0.112, 0.0843, and 0.043 g C g^{-1}, respectively. For maintenance respiration, the coefficient was estimated equal to MRR_{fruit} = 1.15 10^{-3} ± 1.1 10^{-4} g C g^{-1} day^{-1} (n = 30). This coefficient of maintenance respiration was close to those estimated for peach, cucumber, tomato, and lettuce, equal to 6.7 10^{-4} g C g^{-1} d^{-1} (Dejong and Goudriaan, 1989), 4.1 10^{-3} g C g^{-1} d^{-1} (Marcelis and Baan Hofman-Eijer, 1995), 3.3 10^{-3} g C g^{-1} d^{-1} (Walker and Thornley, 1977) and 2.6 10^{-3} g C g^{-1} d^{-1} (Van Iersel, 2003), respectively.

The mean calculated light saturated photosynthesis decreased by about 10 % in leaves of the 50 leaves per fruit treatment when compared to leaves of the 25 leaves per fruit treatment, and by about 22 % in leaves of the 100 leaves per fruit treatment when compared to leaves of the 50 leaves per fruit treatment (Figure 1). Those differences according to the treatments were close to those noted for net assimilation on mango leaves (Urban *et al.*, 2002). Regardless of the treatments, as demand increased, the light-saturated photosynthesis increased (Figure 1). Parameters relating light saturated photosynthesis and fruit demand in Equation 1 were estimated to be p_2 = 33.23 ± 11.91 µmol CO_2 m^{-2} s^{-1}, and p_1 = 3.85 ± 0.57 µmol CO_2 m^{-2} s^{-1} g C^{-1} (n = 60). The value of P^*_{max} fixed according to our measurements of net assimilation was in the same range than values estimated on peach leaves (Ben Mimoun *et al.*, 1996). The estimated parameters linking net photosynthesis response to the photosynthetically active flux

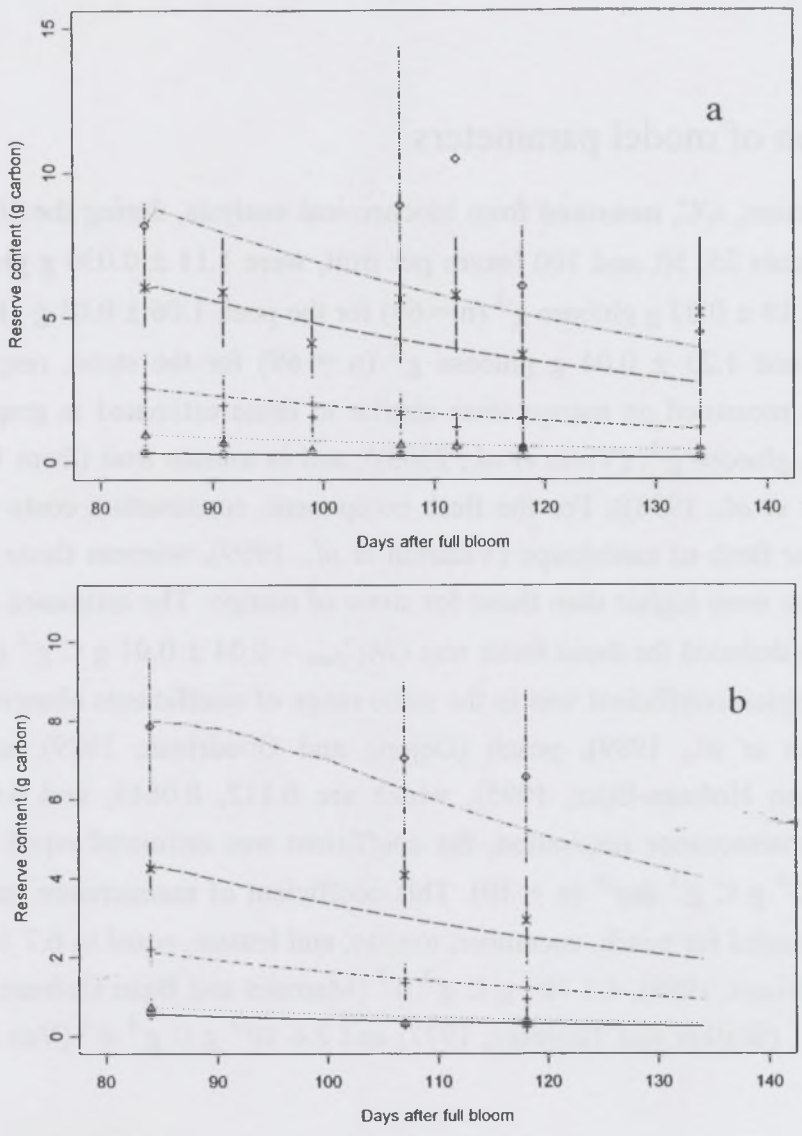

Figure 3: Observed (symbols) and predicted (lines) values of reserve content (g carbon) in leaves (a) and stem (b), for five leaf-to-fruit ratio treatments, 10 (O), 25 (Δ), 50 (+), 100 (×), and 150 (◊). Vertical bars represent standard deviation of measurements.

density were p_3 = 0.483 ± 0.074 (n = 289), and p_4 = 0.034 ± 0.007 (n = 289). For shaded leaves the function g(PPFD) was $PPFD_{shaded} = 0.0529 \cdot PPFD_{sunlit}$ (R^2 = 0.96, n = 142).

We obtained a base temperature of 16.0 °C, which is in the range of base temperatures already found for mango fruit: from 0.33°C (Mosqueda-Vasquez and Ireta-Ojeda, 1993) to 17.9°C (Oppenheimer, 1947). The values of parameter estimates of the potential fruit growth obtained from seasonal fruit dry mass in non-limiting growth were RGR_f^{ini} = 0.0105 ± 0.0003 dd^{-1} (n = 384), a = 16.736 ± 1.637 (dimensionless), and b = 0.624 ± 0.036 (dimensionless). The initial relative growth rate was of the same order of magnitude as the one estimated for peach fruit (Lescourret *et al.*, 1998) which was equal to 0.009 dd^{-1}. In conditions of potential fruit growth, the predicted fruit dry masses were in good accordance with the observations, as shown in Figure 2; the regression coefficient (0.97) was close to 1, and the R-square coefficient was 0.95.

Parameters of reserve mobilisation, r_4 (mobile fraction of reserves in the leaves), and r_5 (mobile fraction of reserves in the stem), obtained by model calibration with data from three various leaf-to-fruit ratios (25, 50, and 100) in the 2000 growing season, were found to be equal to 0.0162 and 0.0164, respectively. These parameters values allowed to predict with a good accuracy the seasonal changes of reserve content in stem and leaves assessed with the data set used for model adjustment (treatments 25, 50, and 100 leaves per fruit on Figures 3A and 3B), and with an independent data set (treatments 10 and 150 leaves per fruit). The dynamic of reserve content in leaves and in stem tended to decrease during fruit growth in all treatments (Figures 3A and 3B).

3.2 Model test

The model was tested against all data sets obtained during 2000, 2001, and 2002 growing season for each leaf-to-fruit ratio. The corresponding local conditions, climate, fruit dry mass at the first date of measurement, and the mean of the measured initial stem dry mass, initial part of reserve in the stem and in the leaves, were used as input data to run the model. For fruit growth assessed on a given fruit during all the season, the individual fruit growth predicted by the model was compared to individual fruit dry mass measured at each date of measurement. For 'destructive' data sets (Figures 4 and 5) the simulated mean fruit growth was compared to the measured mean fruit growth. To represent the deviation of fruit dry mass for 'destructive' data set, the simulations were made with all initial fruit dry masses measured for each data set.

The results of the various simulations were globally satisfactory, for both the different leaf-to-fruit ratios and the different years. For high leaf-to-fruit ratios, 100 and 150, used to estimate

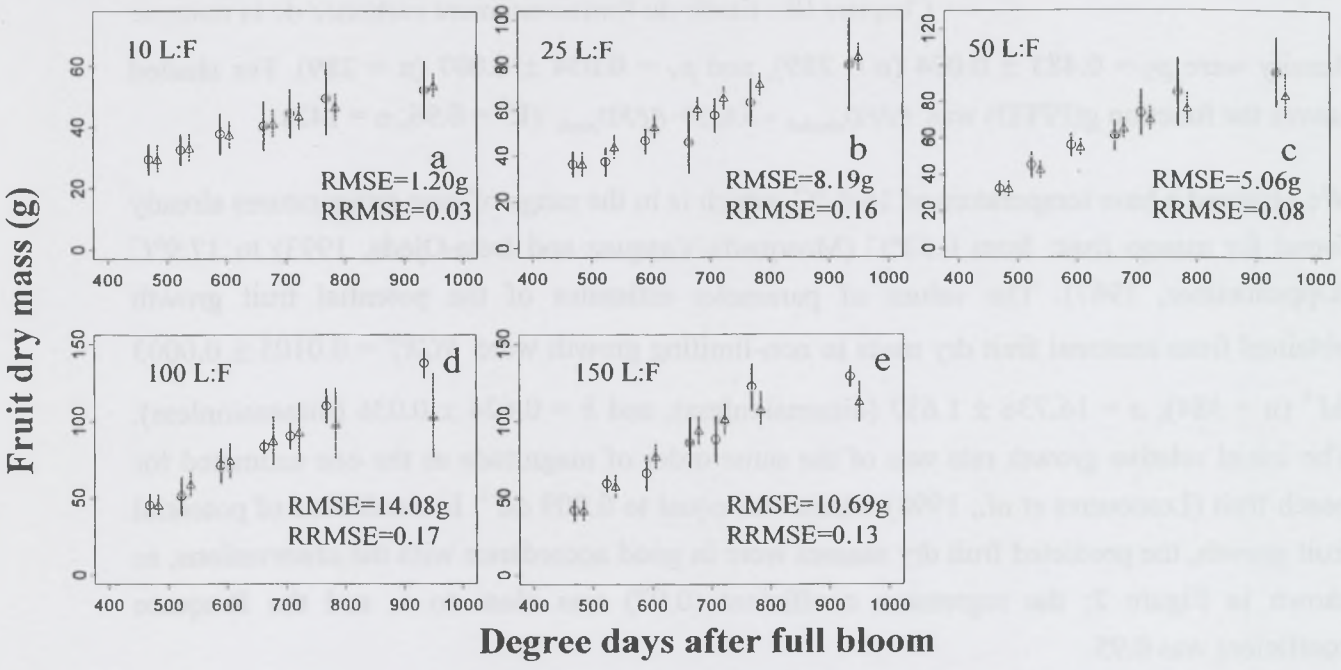

Figure 4: Fruit dry mass for five leaf-to-fruit ratios (L:F), 10 (a), 25 (b), 50 (c), 100 (d), and 150 (e) as a function of degree days. Fruit growth was obtained on 'destructive' measurements in 2000, originated from the first flowering. For each shoot bearing, the mean and the deviation of observed (O and full line) and predicted (Δ and dotted line) data were presented. The root mean squared error (RMSE) and the relative mean square error (RRMSE) were calculated for each data set.

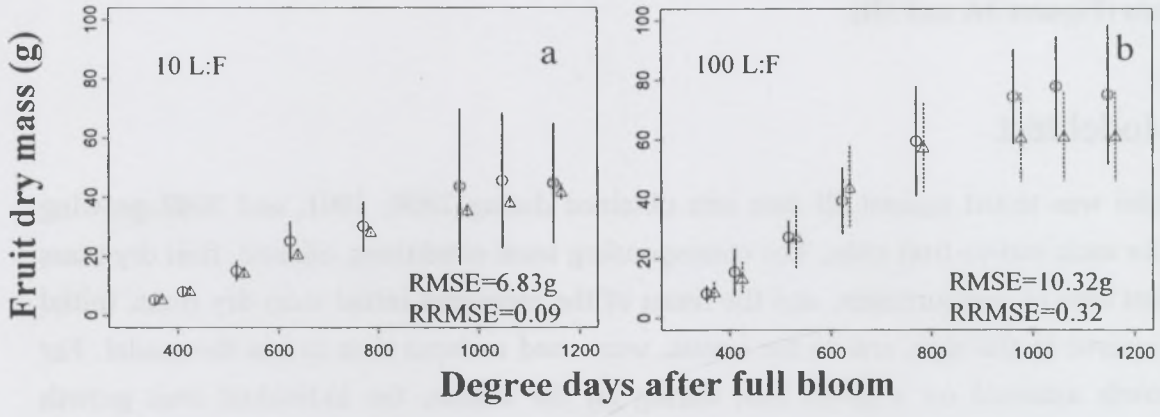

Figure 5: Fruit dry mass for five leaf-to-fruit ratios (L:F), 10 (a) and 100 (b) as a function of degree days. Fruit growth was obtained on 'destructive' measurements in 2001, originated from the unique flowering. For each shoot bearing, the mean and the deviation of observed (O and full line) and predicted (Δ and dotted line) data were presented. The root mean squared error (RMSE) and the relative mean square error (RRMSE) were calculated for each data set.

parameters of potential fruit growth (Figures 5b, 6a, 6b, 7a, 7b, and 7c), the fit of the model was good, as the RRMSE value was included between 8 and 18 %, except the 2001 data set for which simulations from treatment 100 leaves per fruit under-estimated observations and the RRMSE value was close to 30 % (Figure 5b). However, the same year, at harvest the deviation between mean fruit dry mass predicted and observed was about 10 g for fruits weighed 45 g (Figure 5b), and the variability of fruit dry mass, which was large this year, was well reproduced by the model. For the destructive data set of 2000, and especially the treatments 25, 50, and 100, used to estimate parameters of reserves mobilisation, the quality of adjustment was good (Figures 8b, 8c, 8d). The RMSE value for all independent data set was generally low compared to the mean of the observed dry mass. The mean fruit dry mass varied between 10 g to 80 g (Figures 4a, 5a, 6a, 6b, 8a, and 8b) and 20 g to 125 g (Figure 8e) for low and high leaf-to-fruit ratios, 10, 25, and 100, respectively, while the distance between simulation and measurement, the RMSE value, was about 5 to 8 g, and 2 to 16 g, respectively. The quality of prediction of fruit dry mass among the leaf to fruit ratio treatments by the model was good, as the relative RRMSE value, on independent data set, was lower than 20 %. However, in several instance the variability of measurements was not always well predicted (Figures 4a, 4b, 5a, 6a, 6b, and 8a).

3.3 Analysis of model sensitivity to parameters

A sensitivity analysis was performed using the environmental conditions of the growing season in 2000, which extended from 67 to 119 days after full bloom, for two contrasting leaf-to-fruit ratios, corresponding to 10 and 100 leaves per fruit. Sensitivity of the fruit growth rate, calculated between the beginning and the end of the measurements, was investigated (Table 2). The model was very sensitive to the parameters of potential fruit growth, especially the initial fruit weight at about 350 degree days, DM_f^{ini}, used to calculate the maximal final dry mass, regardless of the treatments. Variation in a and b, two other parameters required to calculate the potential dry mass at harvest, had also an effect on fruit growth rate, mainly for fruits from the 100 leaves per fruit treatment, corresponding to sink limiting condition. The model was less sensitive to the other parameters of potential fruit growth and fruit demand, RGR_{ini} and GRC_{fruit}, and to parameters required for maintenance respiration and reserve mobilisation. Concerning parameters of carbon assimilation by leaves, the fruit growth rate was very sensitive to parameter p_2, and to a lesser extent to p_1, p_3, and p_4, mainly for fruits from 10 leaves per fruit, corresponding to source limiting condition. Variations in parameters of maintenance respiration and reserve mobilisation did not affect fruit growth rate, regardless of the treatments.

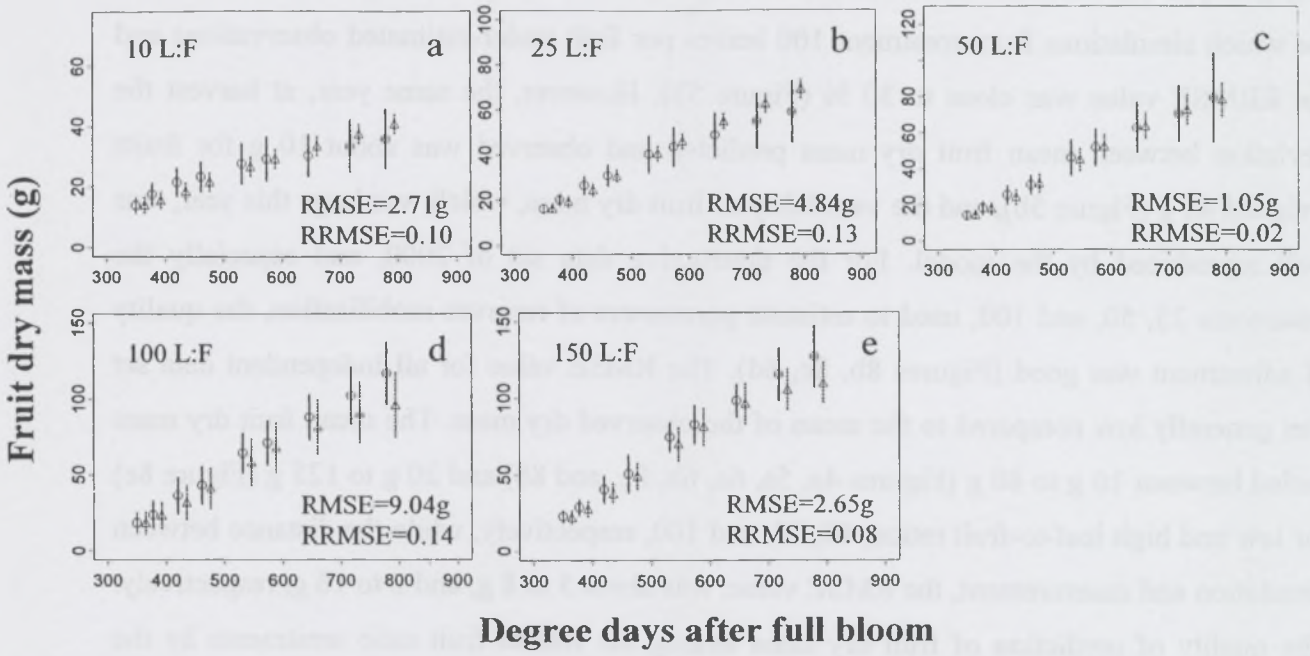

Figure 6: Fruit dry mass for five leaf-to-fruit ratios (L:F), 10 (a), 25 (b), 50 (c), 100 (d), and 150 (e) as a function of degree days. Fruit growth was monitored on same fruit along the season in 2000, originated from the first flowering. For each shoot bearing, the mean and the deviation of observed (O and full line) and predicted (Δ and dotted line) data were presented. The root mean squared error (RMSE) and the relative mean square error (RRMSE) were calculated for each data set.

3.4 Contribution of the effects of climate, initial fruit dry mass, and leaf-to-fruit ratio on fruit growth and underlying physiological processes

The contribution of the different factors and of their interactions to the variance of the studied variables was presented in Table 3. The three main factors affected significantly all the studied variables. The contribution of the initial fruit dry mass was the highest for all sink variables, as respiration (about 93 %), demand (71.5 %) and growth rate (89.8 %) of the fruit, and for stem reserves mobilisation too (about 67.6 %). The contribution of the leaf-to-fruit ratio was large for leaf photosynthesis and leaf reserves mobilisation, less important for fruit respiration and demand, and almost null for fruit growth rate although the effect was significant. However, the same experimental design with more contrasted leaf-to-fruit ratio levels (i.e. 25 and 100 leaves per fruit) showed that the leaf-to-fruit ratio could contribute for more than 70 % to the fruit growth rate variability (data not shown). In that case, the contributions of the other source/sink factors and of the climate were minimised. The seasonal average of daily photosynthesis was 30 % higher in leaves from 50 than from 100 leaves per fruit. For reserves, the mean balance over the season between mobilisation and accumulation was almost null in leaves from 50 leaves per fruit, while it was positive in leaves from 100 leaves per fruit. The contribution of the interaction between leaf-to-fruit ratio and initial fruit dry mass was close to 10% for the fruit demand and the reserve mobilisation in stem. The contribution of the last factor, the climate, was globally the lowest of the three factors. It was especially low for the fruit respiration and the mobilisation of leaf and stem reserves. The contribution of climate to fruit demand was close to 5 %. The largest contribution of the climate concerned photosynthesis (about 6.2 %) and the fruit growth rate (about 9.3 %). Fruit growth length depended on the climate, especially on temperature and also the sum of degree days, as the end of simulations, at 1100 degree days, varied to 23 days among the climate data. The contribution of the interaction between the climate and every other factor was weak.

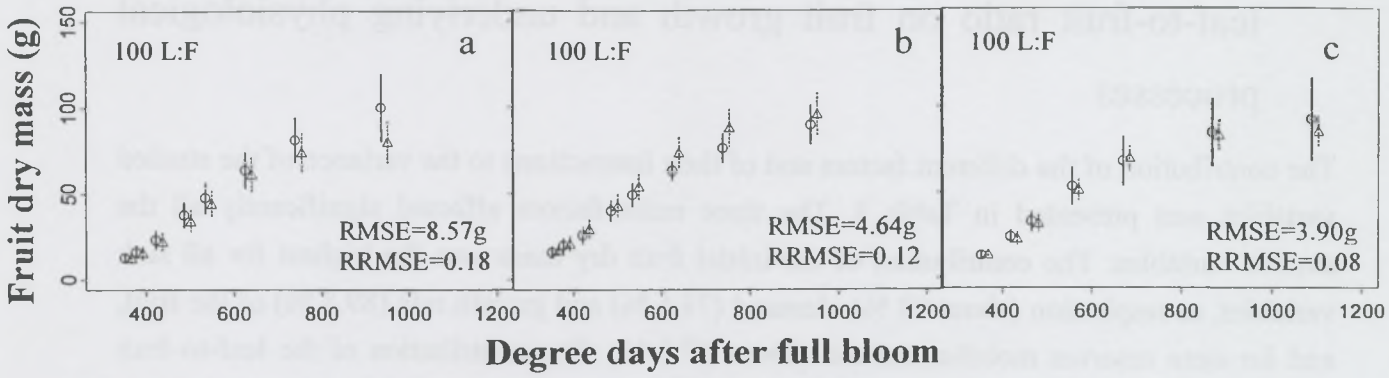

Figure 7: Fruit dry mass for one leaf-to-fruit ratio (L:F), 100 as a function of degree days. Fruit growth was monitored on same fruit along the season in 2002, originated either from the first flowering, on orchards 1 (a) and 2 (b), or from the second flowering on orchard 2 (c). For each shoot bearing, the mean and the deviation of observed (O and full line) and predicted (Δ and dotted line) data were presented. The root mean squared error (RMSE) and the relative mean square error (RRMSE) were calculated for each data set.

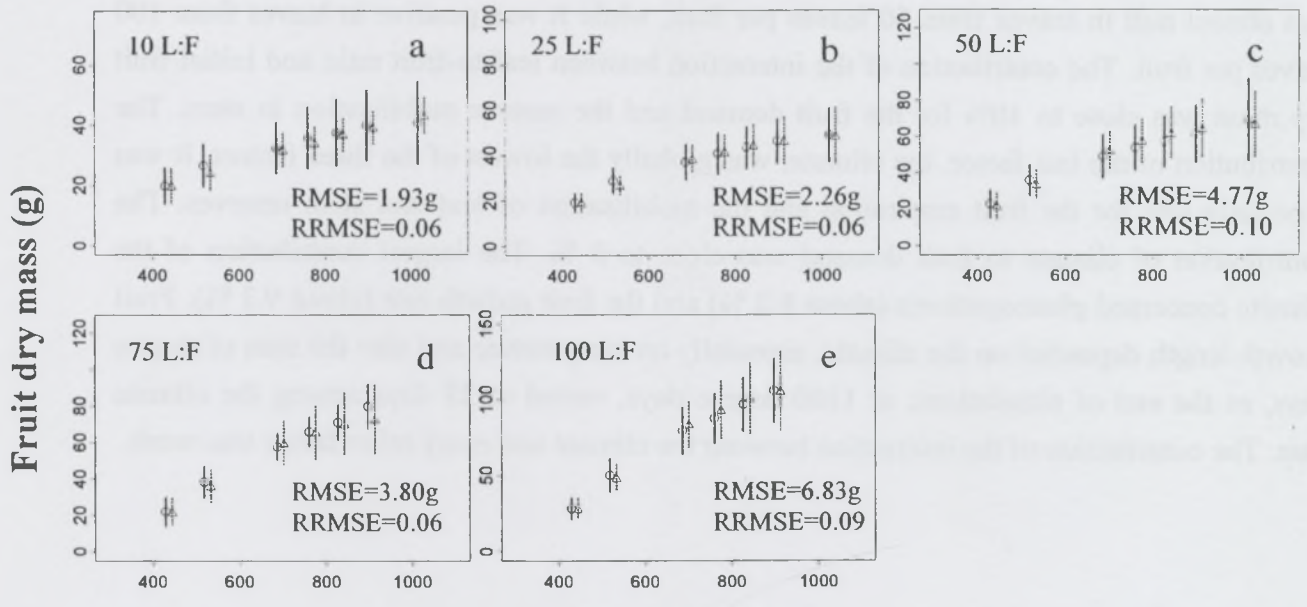

Figure 8: Fruit dry mass for five leaf-to-fruit ratios (L:F), 10 (a), 25 (b), 50 (c), 75 (d), and 100 (e) as a function of degree days. Fruit growth was monitored on same fruit along the season in 2000, originated from the second flowering. For each shoot bearing, the mean and the deviation of observed (O and full line) and predicted (Δ and dotted line) data were presented. The root mean squared error (RMSE) and the relative mean square error (RRMSE) were calculated for each data set.

4 Discussion

4.1 Quality of adjustment and prediction of the model

The predictive quality of the model, assessed on various experimental situations (different leaf to fruit ratio treatments) during three successive years, was good. This model allows to predict the main processes involved in the growth of a fruit knowing the leaf-to-fruit ratio of the studied shoot bearing fruit, which is easily assessed by thinning, and allows to simulate the variability between shoots and between years according to the initial fruit dry mass and to the environmental conditions. The observed variability of fruit dry mass was not always well predicted. It could be due to the light environment of the shoot which was not assessed for each fruit studied. The contribution of the shoot light environment to the fruit weight at harvest on peach fruit was noted to be lower than that of the leaf-to-fruit ratio and initial size of leafy shoot, but this contribution was all the same significant (Génard *et al.*, 1998). This fruit growth model studied here is capable to predict accurately regardless of the treatment, the dynamic of the pool of carbohydrates stored in leaves and stems, this level reflecting the source/sink balance of the system (Iglesias *et al.*, 2002; Layne and Flore, 1993).

4.2 How the initial fruit dry mass influences source/sink relationships?

Our model emphasizes the influence of cell number on fruit growth as demonstrated by several authors (Goffinet *et al.*, 1995; Ho, 1992; Jackson and Coombe, 1966) by relating the potential fruit mass to the early fruit size assessed after the cell division phase. The result of sensitivity analysis shows that the model is very sensitive to the parameter DM_f^{ini}. The initial fruit dry mass seems to be strongly implicated in source/sink balance, because, from results of the virtual study, this parameter has a larger contribution for the simulated fruit growth rate than other source/factor like leaf to fruit ratio, and than climate too. Using the initial fruit dry mass to calculate the maximal final dry mass allows to predict the variability observed between years, especially between 2000 and 2001, two years with profoundly different rates of fruit growth. A limited fruit growth was noted in 2001, regardless of the treatments, but a lower initial fruit dry mass too. This small size at the early stage of development could be due to resources limitation during the cell division phase. It has been observed that fewer cell divisions in fruits reduces subsequently their size and potential growth (Westwood, 1967). In apple, Stanley *et al.* (2000) found that under conditions of non-limiting growth after the cell

Table 2: Sensitivity of the mean fruit growth rate to ± 20% variation of the model parameters. Values are expressed as a percentage of the reference condition (see 'Materials and Methods'). The simulations used for the calculation of the fruit growth rate were performed on fruits from treatments 10 and 100 leaves per fruit during the 2000 growing season.

	Parameter	Level of Variation (%)	Fruit Growth Rate	
	Leaf to fruit ratio		10	100
Carbon assimilation by leaves				
	p_1	+ 20	+3	+1
		- 20	-5	-4
	P^*_{max}	+ 20	+16	+1
		- 20	-19	-3
	p_3	+ 20	-1	0
		- 20	+1	0
	p_4	+ 20	+4	0
		- 20	-6	-1
Maintenance respiration				
	MRR_{stem}	+ 20	-2	0
		- 20	+2	0
	MRR_{leaves}	+ 20	-2	0
		- 20	+2	0
	MRR_{fruit}	+ 20	-3	0
		- 20	+3	0
	Q_{10}^{leaves}	+ 20	-1	0
		- 20	+1	0
	Q_{10}^{stem}	+ 20	-1	0
		- 20	+1	0
	Q_{10}^{fruit}	+ 20	-1	0
		- 20	+1	0
Fruit demand				
	RGR_{ini}	+ 20	+3	+3
		- 20	-4	-8
	DM_f^{ini}	+ 20	+16	+14
		- 20	-16	-16
	a	+ 20	+1	+19
		- 20	-2	-23
	b	+ 20	+2	+32
		- 20	-3	-36
	GRC_{fruit}	+ 20	-2	0
		- 20	+2	0
	c_{fruit}	+ 20	-12	-2
		- 20	+16	+1
Reserve mobilisation				
	r_4	+ 20	0	0
		- 20	0	0
	r_5	+ 20	+1	0
		- 20	-1	0

division phase, fruit mass at harvest was well correlated to fruit mass 50 days after pollination, which is in the same order of magnitude as our date for determining the initial fruit dry mass. In kiwifruit, measurements made 50 days after anthesis can explain nearly 75% of the variation of fruit growth (Hall *et al.*, 1996).

The main part of the fruit respiration was also explained by the initial fruit dry mass, as fruit dry mass and fruit growth rate are directly linked to the expression of maintenance and growth respiration, respectively. The large contribution of the initial fruit dry mass to the fruit demand, resulted from simulations, is due to the importance of the past growth in the expression of this variable (equations 2 and Appendix 2, equation 4). Moreover, this contribution could be explained too by using directly the initial fruit dry mass to compute the potential fruit growth and also the fruit demand (equations 2 and 3).

4.3 How the leaf to fruit ratio influences source/sink relationships?

The variations of simulated reserves in treatments 10 and 25 leaves per fruit were in accordance with results from studies on leaves of cherry and citrus trees showing that carbohydrates content decreased and is low in source-limiting conditions (Iglesias *et al.*, 2002; Layne and Flore, 1993). It was also noted that concentrations of storage sugars, like starch, were high in leaves from light crop load in apple (Wünsche *et al.*, 2000) and pecan (Marquard, 1987) trees, as they were in mango leaves from treatment 100 leaves per fruit. This high level of sugars in leaves suggests that all assimilates produced by leaf photosynthesis were not totally used by the fruit. This storage is the result of the inability of sink tissues to use photoassimilates, which is referred to as a limitation of sink strength (Warren Wilson, 1972). The contribution, noted from simulations, of the leaf-to-fruit ratio to the fruit growth rate was very weak, whereas its contribution to the leaf photosynthesis was close to 68 %. Increasing the leaf-to-fruit ratio from 50 to 100 leaves per fruit increased source size and also the production of assimilates of the bearing shoot. However, there was not a great increase of fruit size. Those processes at source and sink levels confirmed that in non-limiting supply of carbon, i.e. high leaf-to-fruit ratio, the fruit growth rate is limited by the sink, as it has already been reported by Wareing and Patrick (1975). This sink limitation was balanced by the buffer role of reserves, as it has already been noted in sour cherry trees (Layne and Flore, 1993), and in alfalfa (Baysdorfer and Bassham, 1985). The excess of carbohydrates produced by photosynthesis was mainly stored in leaves in the 100 leaves per fruit treatment, as shown by simulated and measured reserves content.

These changes of sink/source balances according to leaf-to-fruit ratio or crop load are generally associated with alterations in source activity (Wünsche *et al.*, 2000) which result in a significant decrease in leaf photosynthesis observed in mango by increasing leaf-to-fruit ratio and on peach (Ben Mimoun *et al.*, 1996), grapevine (Naor *et al.*, 1997), and apple

(Palmer, 1992). This relationship was well represented by the relationship between fruit demand and light saturated photosynthesis implanted in the model. Several studies expressed that end-products of carbon dioxide assimilation results in the feedback inhibition of photosynthesis (Goldschmidt and Huber, 1992; Iglesias *et al.*, 2002). Lescourret *et al.* (1998) chose to use in their model of fruit growth a direct relationship between the level of reserves in the leaves and light saturated photosynthesis. However, Quereix *et al.* (2001) suggested that a phloem-based feedback signal may be involved in photosynthesis regulation, related to sink/source balance.

The importance of the nitrogen content of the leaf is very important for determining the photosynthetic capacity (Harmens *et al.*, 2000). A study on a biochemical model of photosynthesis for mango leaves showed an effect of source/sink relationships on photosynthetic capacity of leaves and on the amount of leaf nitrogen per unit leaf area (Urban *et al.*, 2003). Such biochemical model of photosynthesis may be used to improve the fruit growth model by taking into account the associated changes in source-sink relationships on photosynthetic capacity.

4.4 How the climate influences source/sink relationships?

Results of simulations have shown that the climate contributes to processes involved in fruit growth at the source level (photosynthesis) and at the sink level as well (fruit demand and growth rate). The contribution of climate to photosynthesis was large through (i) a direct effect of light on the rate of electron flow, which depends on the photosynthetically active photon flux density (Farquhar *et al.*, 1980), and (ii) an indirect effect of light on the leaf mass-to-area ratio (M_a), and on the leaf nitrogen content per unit leaf area (N_a) (Urban *et al.*, 2003). Light can modulate the activity or synthesis of certain enzymes involved in carbon metabolism in source tissues (Sicher and Krember, 1985; Vassey, 1989). Photosynthetic light acclimation of leaves results from changes in leaf nitrogen content per unit mass, mass-to-area ratio, and changes in total nitrogen allocation between the various pools of photosynthetic machinery (Evans, 1989; Le Roux *et al.*, 2001). In mango, the main effect of light on photosynthetic acclimation was through the mass-to-area ratio (Urban *et al.*, 2003). This relationship may be represented in a future model.

The contribution of climate to the fruit demand could be due to the daily variation of degree days used to compute fruit demand. The sum of growing degree days from full bloom varied among the season, showing that seasonal temperature profiles differed between seasons and among sites, as it was reported in a study of apple fruit growth occurring in three geographical regions during three seasons in New Zealand (Stanley *et al.*, 2000). In this study, in condition of potential fruit growth obtained by controlling crop load, the response of fruit growth with these changes of temperature between seasons was in accordance with our results from the

virtual study. Fruit growth differed significantly among sites and among season, as it was reported by variance analysis. The fruit demand is also computed with coefficients of growth and maintenance respiration, which are temperature-independent and strongly temperature-dependent, respectively, as reported on tomato by (Walker and Thornley, 1977).

The contribution of temperature to fruit growth can be explained also by the variation of fruit growing length between years observed in the virtual study. This variation of about 23 days was of the same order of magnitude that changes of the mean harvest date of mango fruit (Augais, pers. comm.). Such a variation in the time from pollination to harvest between years was often noted; for apples, it varied between 132 and 157 days after full bloom (Stanley *et al.*, 2000). Others studies suggest that it would be the sum of temperatures during the early stage of development, i.e. the first five to seven weeks, which can be used to predict the length of fruit development period, rather than the sum of temperatures over the whole period (Blanpied and Ben-David, 1970; Lombard *et al.*, 1971; Tromp, 1997). It would be interesting to reassess this observation for mango and if results show that it is more accurate to harvest at a predicted date calculated with this assumption than at 1100 degree days regardless of the year, it would be introduced in the model. The influence of temperature in the early-stages of fruit development was identified in many species, like satsuma mandarin (Marsh *et al.*, 1999; Richardson *et al.*, 1997), and apples (Austin *et al.*, 1999). They suggest that temperature may affect the rate of cell division, whereas temperature may have less impact on the cell expansion phase. In the model developed here, we try to emphasize this effect of early temperatures by computing the maximum fruit dry mass from the initial fruit dry mass which is assessed at a given sum of degree days, proportional to daily changes in temperatures, and not at a given number of days after full bloom.

In comparison with the contribution of source/sink factors to processes involved in fruit growth, that of the climate was often lower. Several studies are consistent with this finding. Blanpied (1964) has found that the correlation coefficient of the relationship between the yearly sum of degree days and the number of days from full bloom to harvest was not significant, and suggests that temperatures did not influence the length of the growing season for Delicious apples. Robinson *et al.* (1991) reported no significant variation in fruit size during ten years on two cultivars of apple. The temperature explained a weak part of the total variation in kiwifruit growth rate, a small but statistically temperature effect was detected (Hall *et al.*, 1996). Those experimental results and our virtual study indicate that although temperature may affect fruit growth, other factors, like those influencing source/sink balance, are much more important.

Conclusion

Experimentations and simulations allowed to study processes involved in mango fruit growth, as source activity, sink demand, fruit respiration, and leaf and stem reserves. This model is

able to account accurately for the variations of those main processes according to the leaf-to-fruit ratio, and to predict with a good accuracy the variation of the fruit dry mass for the various treatments of assimilate supply. The model was very sensitive to the parameters of potential fruit growth, especially the initial fruit mass, regardless of the treatments, and to parameters of carbon assimilation by leaves. The model was less sensitive to parameters required for maintenance respiration and reserve mobilisation in leaves and stem. Moreover, simulations on fruit growth elaborated under various climate conditions and different source/sink factors (initial fruit dry mass and leaf-to-fruit ratio) demonstrate that climate contributes to the variations in leaf photosynthesis, fruit demand, and fruit growth rate, but that contribution is globally lower than that of the initial fruit dry mass and the leaf-to-fruit ratio. It appears that climatic contribution could be more important in particular period of fruit growth, especially in the initial stage. Our results suggested that biochemical model of photosynthesis could be used and determination of the initial fruit dry mass and factors affecting it could be reassess to improve the fruit growth model.

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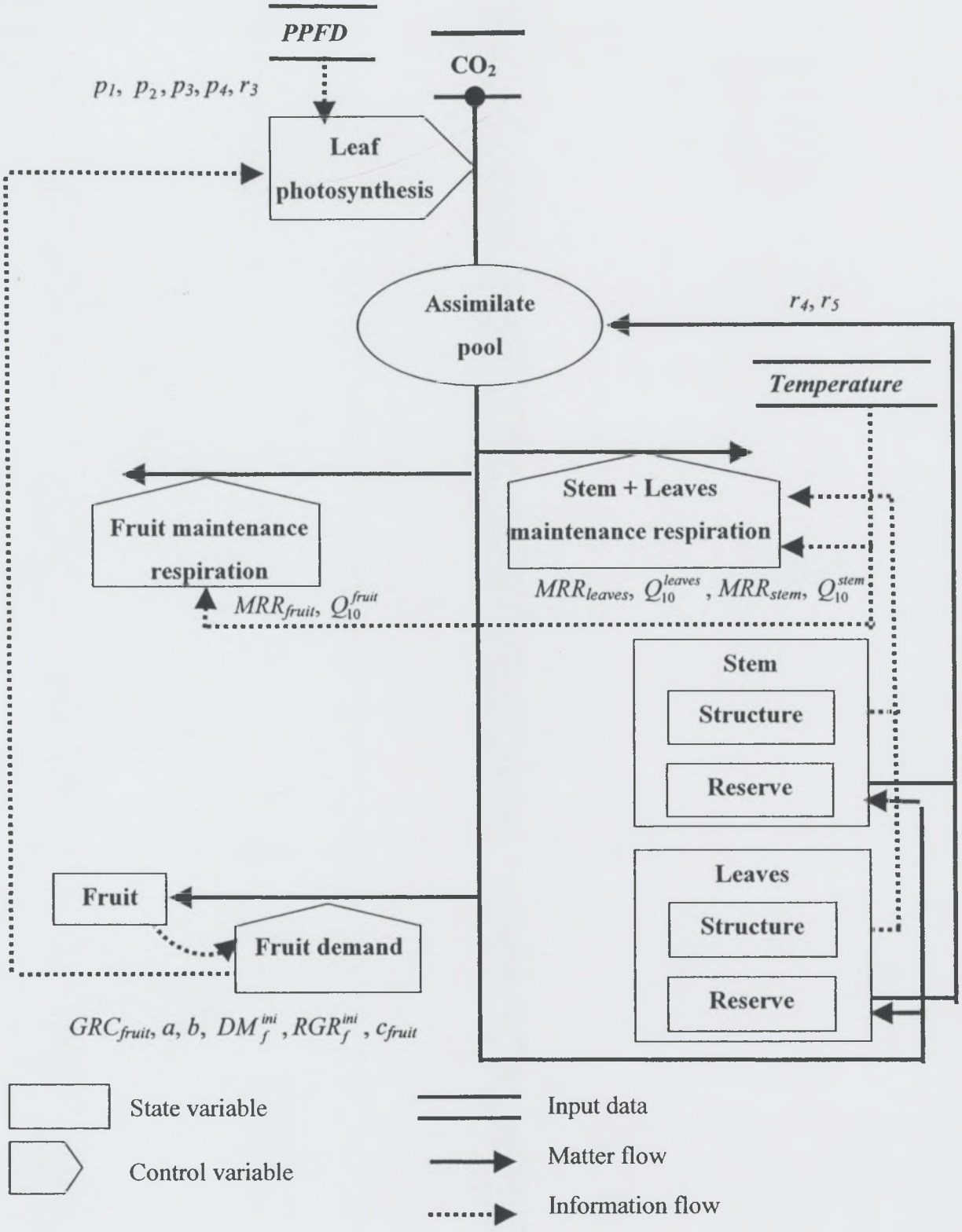
Appendix 1:

Schematic representation of the model. Model parameters are in italics at the level where they are used to computation.



Appendix 2:

- Carbohydrates production:

Response of photosynthesis to the photosynthetically active flux density (PPFD, µmol photon m^{-2} s^{-1}) is calculated as:

$$P_l = \left[\left(P_l^{\max} + p_3\right)\cdot\left(1-\exp\frac{-p_4\cdot PPFD}{P_l^{\max}+p_3}\right)\right] - p_3 \quad (1)$$

For shaded leaves, the same formulation is used, but as a function of g(PPFD).

The amount of carbon produced by leaf photosynthesis, C_l (g carbon day^{-1}), is defined as the sum of hourly photosynthesis by sunlit and shaded leaves:

$$C_l = \left[\left(\sum_{h+} P_l^{sunlit}\cdot LA_{sunlit}\right)+\left(\sum_{h+} P_l^{shaded}\cdot LA_{shaded}\right)\right]\cdot k \quad (2)$$

with, LA the total leaf area (m^2), and k the conversion coefficient (0.0432) from µmol CO_2 s^{-1} to g C h^{-1}.

- Maintenance respiration:

Maintenance respiration, MR (g C day^{-1}), is calculated from the Q10 concept, in the same way for the various organs (i), stem, leaves, and fruit:

$$MR_i = MRR_i\cdot\left(Q_{10}^i\right)^{\frac{\vartheta-\vartheta_{ref}}{10}}\cdot W_i \quad (3)$$

with MRR_i the maintenance respiration rate (g carbon g^{-1} day^{-1}) of organ i at the reference temperature θ_{ref} (°C), Q_{10}^i the Q_{10} value for organ i, θ the mean temperature of the day (°C), W_i (g) the dry mass of the organ i. For leaves, the coefficient is expressed in g carbon g^{-1} h^{-1} and then transforms per day with only the number of dark hours.

- Fruit growth demand:

The daily carbon demand, D_{fruit} (g carbon day^{-1}), for fruit growth is calculated as:

$$D_{fruit} = \frac{\Delta W_f^{pot}}{\Delta dd}\cdot\frac{\Delta dd}{\Delta t}\cdot\left(c_{fruit}+GRC_{fruit}\right) \quad (4)$$

with $\Delta W_f^{pot} / \Delta dd$ (g carbon dd^{-1}) the potential fruit growth rate in terms of degree-days after full bloom (dd), c_{fruit} (g carbon g^{-1}), the carbon content of fruit, and GRC_{fruit} (g carbon g^{-1}) the growth respiration coefficient of fruit.

- Reserves mobilisation:

If the carbohydrates available from current photosynthesis are lower than the amount supplied for maintenance and growth of the system, a mobile amount of reserves (g day^{-1}) can be also used from the leaves, as the following expression:

$r_4 \times RM_{leaf}$ (5)

If it is insufficient, a mobile amount of reserves in stem can be mobilised, which is:

$r_5 \times RM_{stem}$ (6)

where, r_4 and r_5 are the mobile fraction of reserves in the leaf and the stem, respectively, and RM_{leaf} and RM_{stem}, the carbon mass of reserves in the leaf and the stem, respectively.

Chapitre IV : Étude du fonctionnement hydrique de la mangue : An analysis of elastic and plastic fruit growth in response to various assimilate supplies

Chapitre IV : Étude du fonctionnement hydrique de la mangue : An analysis of elastic and plastic fruit growth in response to various assimilate supplies

Dans l'objectif de comprendre le fonctionnement hydrique de la mangue, la croissance horaire en matière fraîche du fruit a été étudiée puis modélisée en s'attachant principalement (i) à prédire l'évolution de la composition biochimique de la chair de la mangue qui permet d'une part de décrire l'élaboration de la qualité du fruit, et d'autre part de calculer la pression osmotique du fruit, une composante de l'état hydrique du fruit, et (ii) à prédire les variations de pression de turgescence, l'autre composante de l'état hydrique du fruit (Léchaudel, M., Lescourret, F., Vercambre, G. and Génard, M. An analysis of elastic and plastic fruit growth in response to various assimilate supplies. Manuscript soumis à *Journal of Experimental Botany*). L'étude de la croissance en matière fraîche de la mangue et de la pression de turgescence des tissus a permis de déduire des paramètres importants indiquant les propriétés d'élasticité et de plasticité des parois de ces tissus. Des lois de variations de ces paramètres sont proposées et un modèle capable de rendre compte des variations de croissance élastique et plastique observées chez la mangue est présenté. Ce modèle est utilisé pour simuler l'effet de la disponibilité hydrique et carbonée sur la croissance et les relations hydriques d'un fruit virtuel.

An analysis of elastic and plastic fruit growth in response to various assimilate supplies

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ABSTRACT

Changes in elastic and plastic components of fruit growth were analysed from a model of fruit growth and under various assimilate supplies. Elastic fruit variation is a function of the elastic modulus as well as of turgor pressure variation. Plastic fruit variation is a function of cell wall extensibility and the difference between turgor pressure and yield threshold pressure. Water relations, at the fruit level, encompassing water potential, osmotic pressure and turgor pressure, were assessed in order to study the reversible and irreversible enlargement process. The model used was partly based on the growth model proposed by Fishman and Génard (1998). The introduction of the reversible elastic enlargement makes it possible to simulate positive turgor pressure during fruit shrinkage. Plastic growth parameters, yield threshold pressure and cell wall extensibility were considered to vary in the model. The model was applied to the mango fruit (*Mangifera Indica* L. cv. 'Lirfa'). Both diurnal and seasonal fruit growth were well simulated in the model. The diurnal variations of water potential, osmotic and turgor pressure were predicted with good accuracy. During the day, plastic growth as described by the model was generally null and shrinkage and swelling were linked to the elastic behaviour of the fruit. Relationships between changes in fruit growth, fruit water relations and fruit composition were compared on the basis of changes in carbon or water supply.

1 Introduction

After a short period of cell division, fruit growth involves the enlargement of fruit cells. For fleshy fruit, this period of enlargement is mainly characterised by a large accumulation of water which results from the balance between incoming and outgoing fluxes (Ho *et al.*, 1987). Water is supplied by the phloem as well as the xylem, and is lost through transpiration. The phloem brings both water and dry matter for fruit growth. Changing the leaf-to-fruit ratio affects fruit growth by altering the supply of carbohydrates to the fruit as well as water accumulation (Léchaudel *et al.*, 2002).

Fruits are submitted to large variations in volume resulting from the balance between these various fluxes. This variation has elastic and plastic components. Elastic fruit variation, which is a reversible process, is a function of the elastic modulus as well as of the variation in the fruit turgor pressure (Ortega, 1990). Plastic fruit variation, which is an irreversible process, is a function of the cell wall extensibility and the turgor pressure at which wall yielding (Green *et al.*, 1971). Water relations at the fruit level, described by osmotic pressure and turgor pressure, are often adequate for studying the reversible and irreversible enlargement process (Boyer, 1985).

Diurnal variation, described by shrinking and swelling, is often less pronounced in fruit than in stem (Huguet and Génard, 1995). However, this does not indicate that fruit elastic deformation is limited but, rather, that the sum of elastic and plastic variations results in continuous enlargement for fruit and in shrinkage with slow growth for stem. When water loss occurs during the day, the fruit shrinks and its turgor pressure is maintained by elastic adjustment (Jones *et al.*, 1985). In an elastic tissue, the decrease of turgor is less than in a rigid tissue for a given loss of water (Tyree and Jarvis, 1982). When the fruit swells, the elastic deformation is mainly caused by the increase of pressure (Proseus *et al.*, 1999). As suggested by Wu *et al.* (1985), the cell wall elasticity is due to the structure and composition of the cell wall. The elastic behaviour can be expected to be purely physical (Proseus *et al.*, 1999).

The role of turgor in extending the walls is well documented. According to Lockhart (1965), turgor pressure above a given threshold pressure leads to cell wall extension. This model of plastic growth introduces two parameters: the yield threshold pressure, Y, and the wall

extensibility, ϕ (Dale and Sutcliffe, 1986). ϕ denotes the irreversible and metabolism-linked deformability of the wall (Cosgrove, 1985). Rapid growth response to changes in plant water status and linear relationships between growth rate and turgor pressure suggested that changes in growth were caused by changes in turgor pressure, and that ϕ and Y were constant. This approximation was adopted by Nonami and Boyer (1990) to describe stem growth and by Fishman and Génard (1998) to simulate the growth of peach fruit. However, some reports have demonstrated a substantial lack of correlation between turgor and growth rate (Schackel *et al.*, 1987), particularly when growth is reduced by plant water deficits while turgor is maintained due to solute accumulation (Michelena and Boyer, 1982; Nonami and Boyer, 1989). Therefore, variation in Y and ϕ could be involved in the complex process of cell expansion.

Studies on the variations of the mechanical properties of walls revealed that wall extension is sensitive to pH and that acids such as auxin induced wall extension and growth (Okamoto *et al.*, 1990). The acid growth theory predicted the existence of wall-loosening proteins, such as wall-bound proteins like expansins, which were reported to facilitate wall extensibility (McQueen-Mason and Cosgrove, 1995). Proseus *et al.* (2000) suggested that factors involving cell metabolism controlled ϕ and the long-term growth of the cell. As the cells mature, expansin activity is reduced (McQueen-Mason, 1995) and alteration in wall structure appears to prevent enzymes from inducing wall extension, probably regulating the cessation of growth. Okamoto-Nakazato *et al.* (2000) isolated two wall-bound proteins which affect the yield threshold through acidification of the cell walls. This suggests that ϕ and Y are expected to be predominantly biochemically controlled and to vary as a function of fruit growth.

Fruit-growth response to carbon supply was studied using a model of fruit volume variation, partly based on the growth model proposed by Fishman and Génard (1998). Fishman and Génard (1998) presented a model dealing with fruit growth, assuming only irreversible cell extension. This model is based on the description of water and sugar accumulation in the fruit. The water inflow is governed by the difference of water potential between the stem and the fruit, by resistance to transfer and by the mechanical properties of the cell wall. The water outflow is proportional to the difference in relative humidity between the air-filled space within the fruit and the ambient atmosphere, and to the conductance to vapour efflux. This model predicts null turgor pressure during fruit shrinkage which conflicts with the positive pressures usually measured in fruit tissues (Mills *et al.*, 1997). This occurrence of null pressures probably results from the lack of a reversible deformation process in the model. A representation of fruit volume variation based on the biophysical water transport in the fruit and including the elasticity of living tissue, as well as the plastic properties, may more accurately simulate the way that the fruit functions.

The reversible elastic component was added to the model by introducing the volumetric elastic modulus as proposed on the cell growth model by Ortega (1990). Regarding plastic growth, the parameters of Lockhart's equation (Y and ϕ) were considered to vary. Estimation of these variations required simultaneous measurements of the fruit growth and of the plant and fruit water status. This was done on mango fruit which is of great economic importance since mango fruit is the number one tropical fruit produced in the world.

The model was tested on diurnal and seasonal dynamics of fruit mass, considering the effect of various assimilate supplies. The simulations of water relations were compared with measurements obtained on mango flesh tissue. The sensitivity of fruit shrinkage and fruit growth rate to the model parameters was studied. The effects of assimilate or water shortage on fruit water relations, fruit growth and fruit composition were compared and discussed.

Table 1: Parameters of the mango model

Parameter	Equation	Value	Significance
ρ (cm h^{-1})	Eq. 2	231.0 ± 5.9	fruit surface conductance
H_f (dimensionless)	Eq. 2	0.996	relative humidity of air space in fruit
γ (dimensionless)		3.65 ± 0.21	empirical parameters relating fruit area (cm^2) to fruit mass (g)
η (dimensionless)	Eq. 3	0.73 ± 0.10	
a.L (g cm^{-2} MPa^{-1} h^{-1})	Eq. 6	1.555 10^{-2} ± 8.3 10^{-4}	product of the ratio of the composite membrane to the fruit area and the hydraulic conductivity of the composite membrane of the fruit for water transport
R (cm^3 MPa mol^{-1} K^{-1})		8.3	gas constant
Y_o (MPa)	Eq. 11	0.0	initial threshold value of hydrostatic pressure
h (MPa g^{-1})	Eq. 10	2.027 10^{-3} ± 3.6 10^{-5}	coefficient of 'wall hardening'
s (MPa h^{-1})	Eq. 10	0.0	coefficient of 'wall loosening'
ϕ_{max} (MPa^{-1} h^{-1})	Eq. 8	1.725 10^{-2} ± 1.31 10^{-3}	cell wall extensibility coefficient
dd_{ini} (degree days) in 2000	Eq. 16	1005 ± 85	degree days after which the cell wall extensibility decreased in 2000
dd_{ini} (degree days) in 2001	Eq. 16	686 ± 108	degree days after which the cell wall extensibility decreased in 2000
τ	Eq. 16	0.966 ± 0.071	rate of cell wall extensibility decrease
ε (MPa)	Eq. 8	15.32 ± 2.14	volumetric elastic modulus

2 Materials and methods

2.1 Plant material

The experimental study was conducted on 11-year-old (in 2000) mango trees of cv. 'Lirfa', grafted on 'Maison Rouge', in Reunion Island (20°52'48''S, 55°31'48''E) during the 2000, 2001 and 2002 growing seasons. The 2000 experimental plot consisted of ten rows, 7 m apart, each of them consisting of nine trees spaced 5 m apart and about 3 m high. The trees observed in 2001 and 2002 were spaced at 5 m by 6 m and were around 3 m high in an adjacent plot.

During the experiment, all trees were irrigated every two days at 100% replacement of evaporation. Six weeks after flowering, about ten to fifteen branches per tree were chosen, representing less than 10% of the total branches of the tree. Their position was randomly chosen on the top of the tree to reduce the variability of light received by leaves which could significantly affect carbon assimilation and fruit growth as well. Branches were girdled by removing a band of bark, 10-15 mm wide, sometimes defruited and defoliated to give 10, 25, 50, 100 and 150 leaves per fruit (with 50 leaves for 5 fruits, 100 leaves for 4, 2 and 1 fruit, and 150 leaves for 1 fruit, respectively). To keep the leaf-to-fruit ratios constant within each treatment, all new emerging leaves were removed. The girdling treatment occurred after the physiological fruit drop, when fruit length was about 5 cm.

2.2 Model presentation

The model is based on a biophysical representation of fruit growth proposed by Fishman and Génard (1998). It simulates hour-by-hour diurnal and seasonal fruit growth after the period of cell division. The fruit has two components. The first component includes the flesh and is described as a single compartment. The second component is the stone. The growth in fresh mass of the stone is deduced from the growth in fresh mass of the flesh by means of an empirical relationship.

The reversible elastic enlargement and the potential relationship between turgor, wall structure and wall metabolism are taken into account by introducing the elastic modulus as proposed in the cell growth model by Ortega (1990) and possible changes in ϕ and Y in the initial Lockhart equation.

A list of the model parameters is presented in Table 1.

The rate of change in flesh water weight (dw/dt) is the sum of the water inflow from xylem and phloem (U) and the water outflow due to transpiration (T_f).

$$\frac{dw}{dt} = U - T_f \tag{1}$$

Fruit transpiration is calculated according to Fishman and Génard (1998):

$$T_f = A_f \cdot \alpha \cdot \rho \cdot (H_f - H_a) \tag{2}$$

where A_f is the fruit surface area (cm^2), α is the saturation concentration of water vapour, $\alpha = (M_w \cdot P^*)/(R \cdot T)$, with M_w = 18 g mol^{-1} the molecular mass of water, R = 8.3 cm^3 MPa mol^{-1} K^{-1} is the gas constant, T is the temperature in Kelvin, P^* (MPa) is the saturation vapour pressure derived from Nobel (1974), ρ is the surface conductance (cm h^{-1}) of the fruit peel, H_f is the relative humidity in the air-filled space within the fruit and H_a is the relative humidity in the ambient atmosphere.

The fruit surface area is related to the fresh mass of the fruit (FM_f, g) by the following empirical relationship:

$$A_f = \gamma \cdot (FM_f)^{\eta} \tag{3}$$

where γ and η are dimensionless parameters.

A composite membrane separates the vessels from the stem close to the fruit and the fruit cell. The reflection coefficient for sugars of this membranes (σ) is assumed to be equal to 1, as proposed Nobel (1974). This implies that solutes and sugars do not enter fruit by mass flow, but only via active uptake. The water inflow (U) from the stem to the fruit and the fruit is therefore:

$$U = A \cdot L_f \cdot [\Psi_s - \Psi_f] \tag{4}$$

where Ψ_f (MPa) is the fruit water potential, with $\Psi_f = P_f - \pi_f$ (5)

P_f (MPa) is the turgor pressure, π_f (MPa) is the osmotic pressure in the fruit, $A = a \cdot A_f$, where a (dimensionless) is the ratio of the area of the membrane to the fruit area, L_f (g cm^{-2} MPa^{-1} h^{-1}) is the hydraulic conductivity between the stem and the fruit including that of xylem and that of phloem ($L_f = L_x + L_p$), and Ψ_s (MPa) is the stem water potential.

The osmotic pressure is obtained by the following equation according to Nobel (1974):

$$\pi_f = R \cdot T \cdot \Sigma_j \left(\left(n_j + n_{aa} \right) / w \right) \quad (6)$$

where n_j is the number of moles of osmotically-active solute j analysed, n_{aa} is the number of amino acids and w is the total volume of water in the flesh (cm^3).

The concentration of total nitrogen in mango flesh was relatively constant during fruit growth - about 0.05 to 0.12 g $100g^{-1}$FM (data not shown). The main nitrogen is in a soluble state in fruit flesh with about two-thirds of total nitrogen in peach (Lobit *et al.*, 2002). The mass of amino acids was considered to be constant during fruit growth. A first approximation of the number of moles of amino acids was calculated using the average molar mass of amino acids found in mango (Hall *et al.*, 1980).

The number of moles of the other osmotically-active solutes was expressed for each one as:

$$n_j = \left(prop_j \cdot DM_{fl} \right) / MM_j \quad (7)$$

where $prop_j$ (dimensionless) is the mass proportion of the osmotically-active solute j (minerals, organic acids and sugars) in the dry mass of the flesh (DM_{fl}, g) and MM_j (g $mole^{-1}$) is the molar mass of the osmotically-active solute j.

The proportion of osmotically-active solute j ($prop_j$) in the flesh dry mass was estimated from results of biochemical analysis by linear regression with the following explanatory variables: (i) the sum of degree days after full bloom (dd), (ii) the dry mass of flesh (DM_{fl}) and (iii) their interaction:

$$prop_j = \delta_j^1 + \delta_j^2 \cdot dd + \delta_j^3 \cdot DM_{fl} + \delta_j^4 \cdot \left(DM_{fl} \cdot dd \right), \quad (8)$$

with $\delta_j^1, \delta_j^2, \delta_j^3, \delta_j^4$ as empirical parameters, depending on the compound j.

The change in flesh volume (V) due to water and dry matter accumulation is:

$$\frac{dV}{dt} = \frac{1}{D_w} \cdot \frac{dw}{dt} + \frac{1}{D_s} \cdot \frac{d(DM)}{dt} = \frac{1}{D_w} \cdot (U - T) + \frac{1}{D_s} \cdot \frac{d(DM)}{dt} \quad (9)$$

where $\frac{dw}{dt}$ and $\frac{d(DM)}{dt}$ are the rates of change in water and dry mass, respectively, and D_w and D_s are the density of water and carbohydrates. The density of the main compounds of dry matter such as citric acid (1.67), glucose (1.56), fructose (1.60) and sucrose (1.58) was around

1.6 (Weast *et al.*, 1984-1985). We used 1.6 for the density of dry matter (D_s) and 1.0 for that of water (D_w).

The change in flesh volume is the result of both plastic and elastic volume variations. The equation representing the elastic deformation of tissues (Ortega, 1985) is added to the classical equation of Lockhart (1965), representing plastic growth:

$$\frac{dV}{dt} = \phi \cdot V \cdot (P_f - Y) + \frac{1}{\varepsilon} \cdot V \cdot \frac{dP_f}{dt} \qquad if\ P_f > Y \tag{10}$$

$$\frac{dV}{dt} = \frac{1}{\varepsilon} \cdot V \cdot \frac{dP_f}{dt} \qquad if\ P_f \leq Y \tag{11}$$

where ϕ ($MPa^{-1}\ h^{-1}$) describes the extensibility of the cell walls, Y (MPa) is the yield threshold pressure and ε is the elastic modulus (MPa). The elastic modulus was considered to be constant in a first approximation.

Combining Equations 9, 10, and 11, the fruit turgor is calculated as:

$$\frac{dP_f}{dt} = \frac{\varepsilon}{V}\left[\frac{A_f \cdot aL_f \cdot (\Psi_s - P_f + \pi_f) - T}{D_w} + \frac{1}{D_s} \cdot \frac{ds}{dt} - \phi \cdot V \cdot (P_f - Y)\right] \qquad if\ (P_f \geq Y) \tag{12}$$

$$\frac{dP_f}{dt} = \frac{\varepsilon}{V}\left[\frac{A_f \cdot aL_f \cdot (\Psi_s - P_f + \pi_f) - T}{D_w} + \frac{1}{D_s} \cdot \frac{ds}{dt}\right] \qquad if\ (P_f < Y) \tag{13}$$

where aL_f is the product of the ratio of the composite membrane to the fruit area and the global hydraulic conductivity to the fruit between the stem and the fruit.

Y and ϕ reflect properties of the cell wall and may be variable as previously suggested. Two processes called "strain-hardening" and "wall-loosening" affect Y according to the following equation (Green *et al.*, 1971):

$$\frac{dY}{dt} = h \cdot \frac{dV}{dt} - s \tag{14}$$

where h ($MPa\ cm^{-3}$) is a parameter that accounts for the hardening of the cell wall in response to stretching and s denotes a process, steady over a given period of time, that softens the wall. The rate of wall loosening (s, $MPa\ h^{-1}$) is probably a complex function of environmental conditions, metabolism and plant hormones actively involved in fruit maturation. It was

initially assumed that s was zero since we consider the period of fruit growth before fruit maturation.

Equation 14 is therefore integrated over a given period of time and becomes, at time t after full bloom:

$$Y(t) = Y_o + h \cdot (V(t) - V_o) \tag{15}$$

where V_o (cm^3) is the flesh volume at t_o, the time at which fruit growth begins, corresponding to full bloom. For the sake of simplification, we considered that V_o and Y_o are equal to zero at t_o and, therefore, $Y(t) = h \cdot V(t)$.

With regard to wall extensibility, ϕ, a correlation between the decrease in wall extensibility and the cessation of growth has been reported (Bütenmeyer *et al.*, 1998). When cells mature, Proseus *et al.* (1999) suggest that ϕ decreases and can reach zero. We propose an equation where ϕ is constant and maximal (ϕ_{max}) until a given time (dd_{ini} in degree days) and then decreases according to a rate parameter (τ):

$$\phi = \phi_{max} \qquad if\ dd < dd_{ini}$$

$$\phi = \phi_{max} \cdot \tau^{(dd - dd_{ini})} \qquad if\ dd > dd_{ini} \tag{16}$$

The main variables, turgor and osmotic pressure were calculated using Equations 6, 12, and 13, leading to the estimation of the different fluxes (water inflow, transpiration). The rates of change of dry flesh mass (input data) were added to Equation 1 (rate of change of water flesh mass), and subsequent integration gave the fresh mass of the fruit flesh. To obtain the variation of the fresh fruit mass, the fresh mass of the stone, established by allometric relationship (see 'Materials and methods'), was added to that of the flesh.

2.3 Measurements for parameter assessment

2.3.1 Fruit surface conductance and hydraulic conductivity of xylem

Measurements of fruit diameter variations were carried out during two experimentations, over three periods of fruit growth, with four replicates, in 2001. Firstly, changes in fruit diameter were monitored on detached fruits which were picked and suspended in the tree canopy at their previous position in order to estimate fruit surface conductance from climatic data as explained in Equation 2. Secondly, diameter changes were recorded on fruits with a girdled

pedicel to stop phloem translocation. The model used estimated the product of the ratio of the composite membrane area to the fruit area and the global hydraulic conductivity of xylem only, since phloem flow does not occur in this fruit, by calibration between predicted and observed fruit volume variations.

2.3.2 Elastic modulus

The elastic modulus of mango fruit was estimated during a period when the net accumulation of fresh matter was close to zero, which occurred during the latter stage of the fruit growth season. During this period, measured variation of fruit volume was assumed to be only due to elastic variation (Equation 11). Measurements of the diurnal variation of flesh volume and turgor pressure were assessed on fruits from the 10- and 100-leaf-to-fruit ratio treatments on one day in 2001 (4th December) and one day in 2002 (17th December), from 5 am to 8 pm. The elastic modulus was estimated using averaged data of flesh volume variation and turgor pressure of each measurement period.

2.3.3 Wall extensibility (ϕ), yield turgor pressure (Y) and conductivity (aL_f)

The turgor pressure and the diurnal variation volume were measured from 5 am to 10 pm, on fruits from the 100-leaf-to-fruit ratio treatment during five periods between 8th November and 29th November in 2002. The relative rate of elastic volume variation was then calculated, taking into account the variation of turgor pressure and using the previously estimated elastic modulus, as described in Equation 11. The relative rate of plastic volume variation was then determined after the elastic extension was subtracted from the total relative rate of volume variation (Equation 10). It was expected that plots of the estimated relative rate of plastic variation versus turgor pressure would result in lines with a slope equal to the maximal wall extensibility, ϕ_{max}, and an intercept with the x-axis and the turgor threshold, Y. With this method, possible variations of ϕ and Y were examined. ϕ_{max} was estimated.

The product of the ratio of the composite membrane area to the fruit area and the global hydraulic conductivity of the fruit, aL_f, and the parameter of "strain-hardening", h, (including the variation of the yield threshold turgor, Y, according to Equation 15) were assessed by calibration of the model. This 'calibration procedure' used averaged data of volume variations, monitored on fruits from the 100-leaf-to-fruit ratio treatment during three periods of about three to four days, between 8th November and 2nd December 2002. Since fruit growth was rapid during this period, the value of ϕ_{max} was used as the wall extensibility value in the model.

Parameters linked to the variation of wall extensibility, τ and dd_{ini} (Equation 16), were estimated by using the model and averaged observed data of the seasonal variation of fruit growth from the 100-leaf-to-fruit ratio treatment in 2000 and 2001.

2.3.4 Allometric relationships

The allometric relationship between the fruit fresh weight and the fruit skin area was studied on 61 fruits picked during the growing season. Parameters relating the fruit surface (cm^2) to the fruit mass (g), as described in Equation 3, were estimated at: $\gamma = 3.65 \pm 0.21$ ($n = 61$) and $\eta = 0.73 \pm 0.10$ ($n = 61$) ($R2 = 0.98$).

The dry mass (DM) and the water mass (WM) of the flesh were related to the fruit diameter (D) by empirical relationships ($DM = 0.8191 \cdot e^{(0.051 \cdot D)}$, $R^2 = 0.90$, and $WM = 14.168 \cdot e^{(0.035 \cdot D)}$, $R^2 = 0.94$, $n = 253$).

The fresh mass of the stone (FM_{stone}) was calculated empirically from the fresh mass of the flesh: $FM_{stone} = 0.1167 \cdot FM_{flesh}$ ($R^2 = 0.72$, $n = 253$).

2.3.5 Parameters of the proportions of osmotically-active solutes

Biochemical analyses used to estimate the parameters of Equation 9 were made on fruits from the 10- and 100-leaf-to-fruit ratio treatments during the 2001 growing season. The fresh pulp was thawed and finely homogenised by a Polytron (PT1600E, Kinematica AG, Switzerland). Concentrations of calcium, magnesium and potassium were determined on the diluted mango juice with a capillary ion analysis (CIA, Waters, Massachusetts, USA). The CIA conditions were UV CAT2 electrolyte, silica capillary, 10-µA current and 20kV voltage, hydrostatic injection, 10 nL sample injected, electro-osmotic flux migration and UV detection (185 nm, mercury lamp). The concentrations of organic acids were analysed by using high-performance liquid chromatography (HPLC, DIONEX Co., Sunnyvale, USA). The conditions were CarbopacPA1 guard-column, IonPacAS11 column, 25µL sample injected, elution by a linear gradient from 0.5mM to 35mM NaOH in 25min, flow rate at 2 mL/min and conductimetric detection (type ED40 equipped with an automatic suppressor: ASRS cartridge). Peaks of organic acids were confirmed by comparison with standard mixtures. Concentrations of sucrose, glucose and fructose were measured using an HPLC system. The HPLC conditions were CarbopacPA1 guard-column and column, 25µL sample injected, isocratic elution by a 200mM NaOH and purified water mixture (85:15, v/v), flow rate at 1 mL/min and

amperometric detection (type ED40). Peaks of sugars were confirmed by comparison with standard solutions. Starch was hydrolysed with amyloglucosidase (14 amyloglucosidase units/ml, Novo Nordisk Bioindustries Ltd., Denmark) and its concentration was determined by a colorimetric dosage of glucose (glucose analysis kit, ref 716251/Boehringer Mannheim, Diffchamb, France).

2.4 Measurements of fruit growth and water relations

2.4.1 Seasonal variation of fruit growth

During the 2000 growing season, six fruits from the five leaf-to-fruit ratio treatments (10, 25, 50, 100 and 150 leaves per fruit) were harvested each week between 15 November 2000 and 4 January 2001. In the second year of the experiment, six fruits from two leaf-to-fruit ratio treatments (10 and 100 leaves per fruit) were harvested every fifteen days between 19 October 2001 and 21 January 2002. For each fruit, the fresh mass and masses of the different fruit components (peel, flesh and stone) were measured. A sample of each component was taken from each fruit, weighed and then dried at 75°C for 48 h, and the corresponding dry masses recorded, whereas the remainder was frozen at -20°C for future biochemical analysis.

2.4.2 Diurnal variation of fruit growth

The diurnal variations of fruit diameter were measured continuously on two fruits from the 10-leaf-to-fruit ratio treatment on a day in 2001, and on four to 11 fruits from the 100-leaf-to-fruit ratio treatment on four to seven successive days in 2002. Changes in fruit diameter were continuously recorded using a linear variable differential transformer (LVDT) mounted on an INVAR frame (Li *et al.*, 1989). All the sensors were connected to a datalogger (21 X datalogger from Campbell Scientific Ltd).

2.4.3 Water relations in the fruit flesh and in the stem

Diurnal variations in fruit water potential and fruit osmotic pressure were measured on one and four days between November and December in 2001 and 2002, respectively. The only measurement day in 2001 and the last day in 2002 corresponded to periods of small growth rate, whereas the three first days in 2002 corresponded to rapid fruit growth. Measurements began between 5 am and 6 am and finished between 8 pm and 10 pm, at approximately three-hour intervals. Fruit water potential was measured using the WP4 dewpoint potentiameter (Decagon Devices, Inc. Pullman, Washington, USA). For each measurement, two fruits from the 10-leaf-to-fruit ratio treatment were used in 2001, and three fruits from the 100-leaf-to-fruit ratio treatment were used in 2002. The water potential was determined on a disc of fruit

flesh of approximately 2.5 cm in diameter. Four replicates per fruit were used. As soon as the water potential was measured, each disc was placed in a freezer. The osmotic pressure of the juice extracted from the thawed fruit was later determined using a vapour pressure osmometer (Wescor, Logan, Utah USA). Turgor pressure was calculated by subtracting osmotic pressure from fruit water potential.

The stem water potential was measured with a pressure chamber. Four hours before the measurements, the leaf was enclosed in a bag wrapped in aluminium. This inhibited leaf transpiration and the water potential in the leaf was in equilibrium with that of the stem at the point of leaf insertion. Measurements were performed on eight to ten leaves for each period of fruit potential measurement.

2.5 Modelling Technique

Simulation of both diurnal and seasonal processes was based on an hourly scale. The model was based on differential equations which were solved numerically by the first order Runge-Kutta method. The model was written using the S-Plus language.

The parameters ε, h, aL_f, τ and dd_{ini} were estimated with the non-linear least squares regression function, which minimises the sum of squared residuals.

The empirical parameters, $\delta_j^1, \delta_j^2, \delta_j^3, \delta_j^4$, used in Equation 9, were estimated by linear regression.

2.6 Description of input data

The climatic data were collected by the local meteorological station located close to the orchard (CIRAD, Saint Pierre). The maximum and minimum daily temperatures were used to assess the sum of growing degree days after full bloom.

Discontinuous measurements of stem water potential using a pressure chamber led to the estimation of an empirical linear relationship (the value of the multiple R-squared was 0.41), linking stem water potential to climatic data (temperature, relative humidity and global radiation), which led to the simulation of continuous stem water potential (data not shown), one of the input data of the model.

The rate of dry matter accumulation in the fruit was derived from data on fruit diameter changes. The daily rate of dry mass was converted into an hourly rate, assuming a constant rate throughout the day, which is consistent with observations of constant sugar

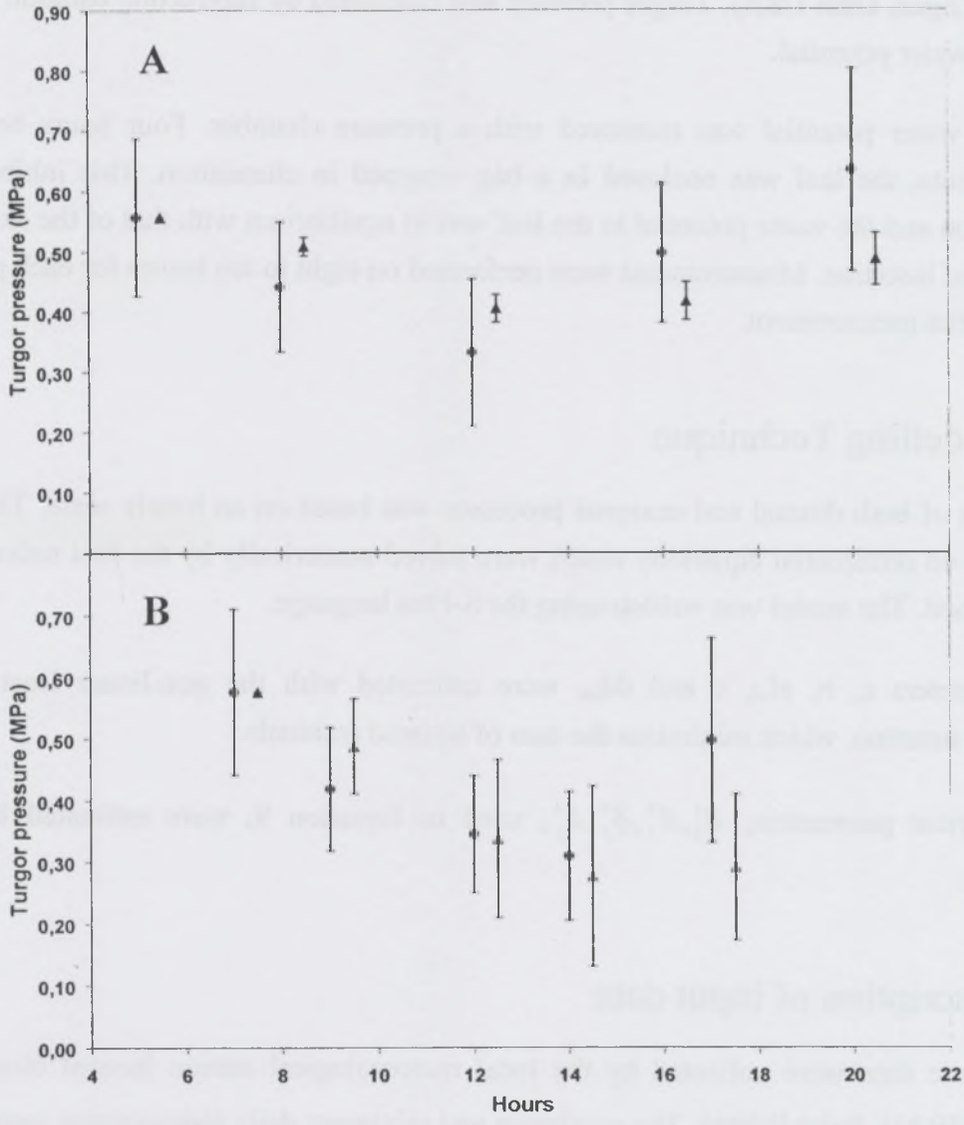

Figure 1: Diurnal changes in fruit turgor pressure from the 10-leaf-to-fruit ratio treatment in 2001 (A) and the 100-leaf-to-fruit ratio treatment in 2002 (B). Circles and triangles indicate observed and simulated turgor pressure, respectively. Each point of turgor pressure is the mean of two (A) and three (B) fruits for measurements, and of two (A) and four (B) fruit volume variations for simulations on the 4th December 2001 and the 17th December 2002, respectively. Vertical bars represent standard deviations.

concentrations in phloem during a day (Sovonick-Dunford, 1986), or simulations of diurnal changes of peach dry weight (Fishman and Génard, 1998).

2.7 Initial conditions

The estimation of the elastic modulus (ε) and the parameters, aL_f and h, required initial values for fruit pressure. The average value of all measurements assessed at predawn on the day of estimation, was determined. When the model was run throughout the season, it also required an initial value for turgor pressure which was determined as being equal to the average value of all measurements assessed at predawn in 2001 and 2002. Initial values for dry and fresh fruit masses were obtained from measurements assessed the day when simulation began.

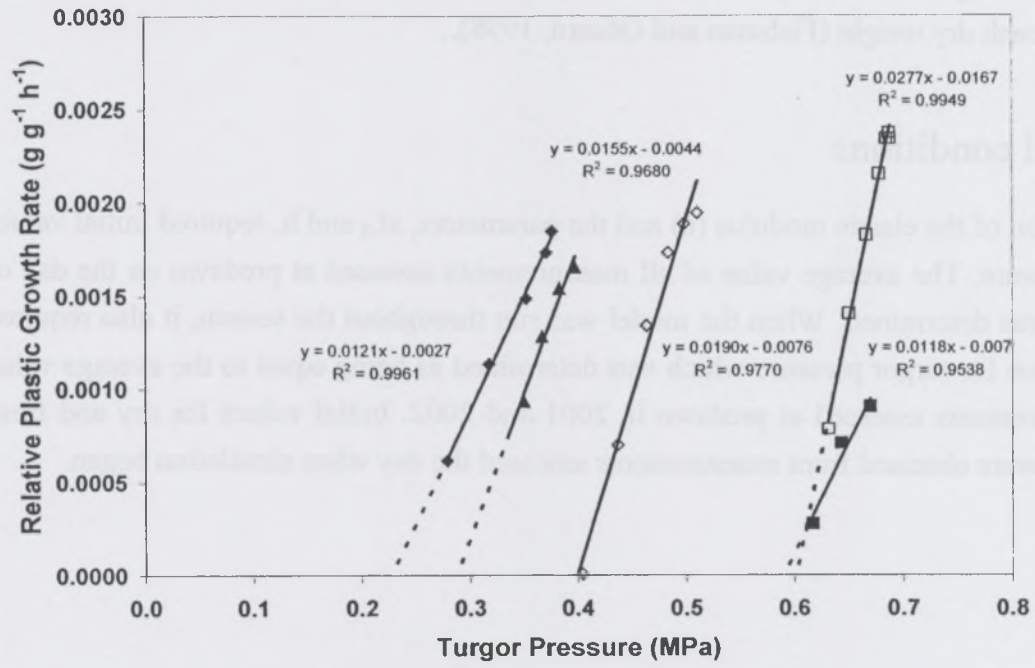

Figure 2: Relative rate of plastic variations of fruit volume as a function of fruit turgor pressure, for five measurement periods. Lines represent linear regressions.

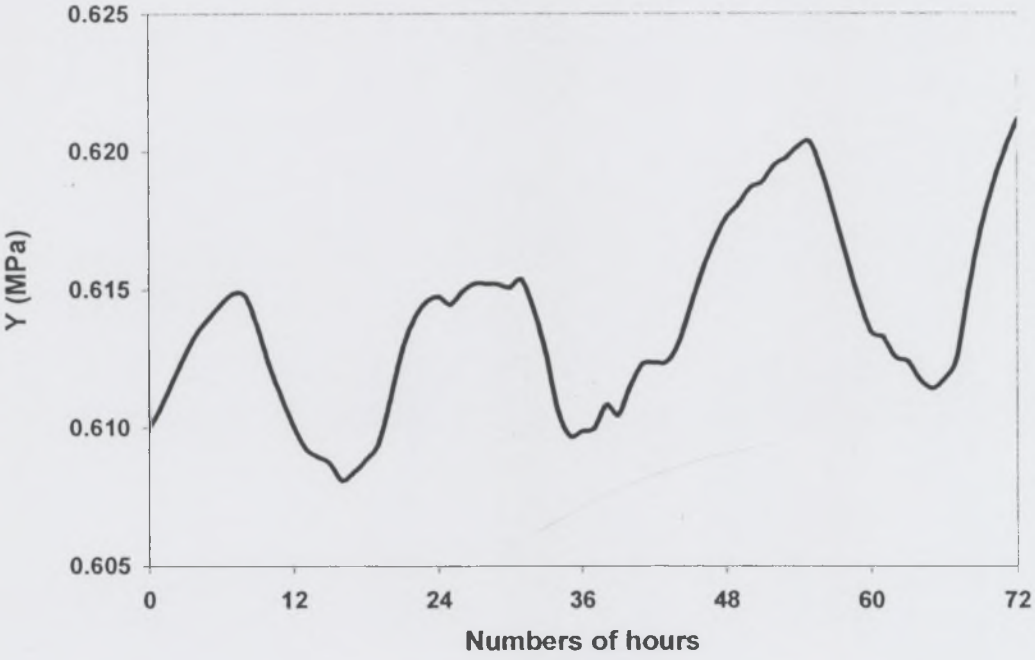

Figure 3: Diurnal dynamics of the yield threshold pressure, Y, simulated from 129 to 131 days after full bloom in 2002.

3 Results

3.1 Estimation of model parameters

The fitted parameter values of the empirical model of flesh composition leading to the simulation of the number of moles of osmotically-active compounds are summarised in Appendix 1. The relationship between the simulated and observed number of moles of the total solutes was close to the first bisector and the R-squared value was equal to 0.7.

The estimated fruit surface conductance was $\rho = 231.0 \pm 5.9$ cm h^{-1} ($n = 12$). This value is a little higher than the surface conductance estimated on mature green mangoes cv. Keitt (Fishman *et al.*, 1996) and in the range of fruit surface conductance values of various peach varieties, from 62 to 901 cm h^{-1} (Lescourret *et al.*, 2001).

We obtained an elastic modulus of about 15.32 ± 2.14 MPa for fruits from the 10- and 100-leaf-to-fruit ratio treatments over two growing seasons. This estimate is within the range of values obtained for cells of higher plant tissues (0-30 MPa), apple fruit cells (2-16 MPa) and stem tissue (2-50 MPa), as it has been reported (Dale and Sutcliffe, 1986; Génard *et al.*, 2001; Steudle and Wieneke, 1985; Tyree and Jarvis, 1982). When given as an input for diurnal volume variations, the simulation of turgor pressure underestimated the last measurement of the day but accurately described the mean of the observations during the rest of the day (Figure 1). The relationship between simulated and observed turgor pressure was close to the first bisector and the R-squared value was equal to 0.7. The variability was well simulated on the second day of measurement (Figure 1B) and, to a lesser extent, on the first one (Figure 1A), due mainly to the weak variability of volume variations monitored.

Turgor pressure measurements were plotted against the corresponding plastic relative growth rate (Figure 2). The plastic relative growth rate increased with turgor pressure. The relationship was linear ($R^2 > 0.95$), regardless of the situation (Figure 2). The slope of regression lines was similar, indicating that the wall extensibility was almost constant during the five measurement periods in 2002 (between 81 and 103 DAB, corresponding to 454 and 625 degree days, respectively). The mean of the different slope values, 0.01725 ± 0.00131 MPa^{-1} h^{-1}, was used in the model as an estimate of ϕ_{max}. It was lower than the value obtained

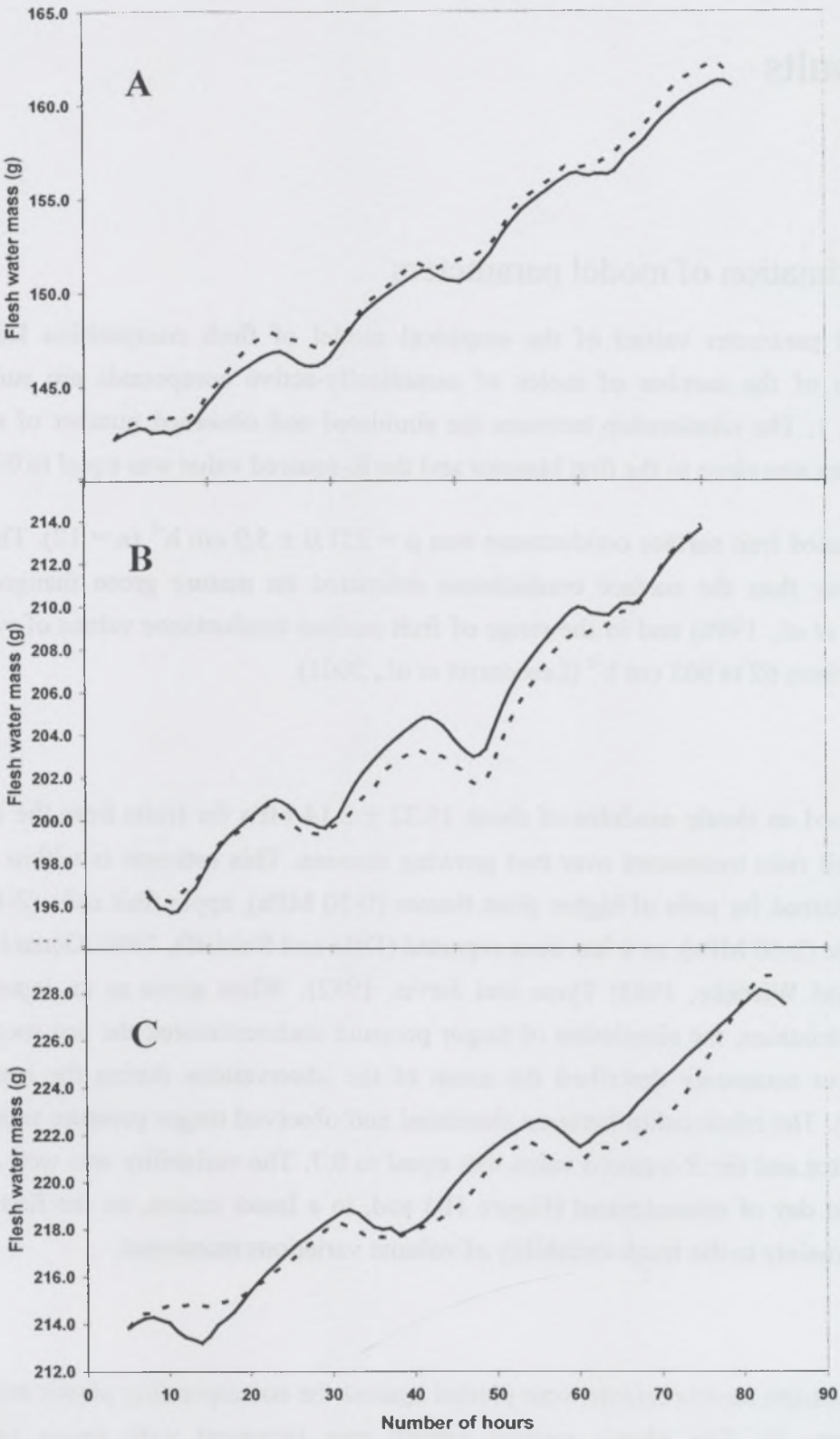

Figure 4: Variations of flesh water mass on fruits from the 100-leaf-to-fruit ratio treatment used for model calibration, for three measurement periods on the 8th, 25th and 29th November 2002, respectively. Unbroken lines and broken lines represent observed and simulated mass, respectively.

on leaves (Serpe and Matthews, 1992) and generally lower than the published results on cell studies - about 0.03-0.2 h^{-1} MPa^{-1}. The estimated value was also lower than the value used in the model of Fishman and Génard (1998) for peach fruit.

The estimations showed that τ was constant, whereas dd_{ini} varied with the year when the experiment was performed. The fitted parameters were $\tau = 0.966 \pm 0.071$ and $dd_{ini} = 1005 \pm 85$ degree days in 2000, and $dd_{ini} = 686 \pm 108$ degree days in 2001, which corresponded to the beginning of the growth slowdown for each growing season.

The intercept of the linear relationship between plastic relative growth rate and turgor pressure with the x-axis varied from 0.22 to 0.60 MPa (Figure 2) which is consistent with our hypothesis about the variability of the yield threshold, Y.

The parameter h from the Y function in Equation 14 was estimated to be $h = 2.027\ 10^{-3} \pm 3.6\ 10^{-5}$ MPa cm^{-3}. Simulation of Y from 129 to 131 days after full bloom for fruit from the 100-leaf-to-fruit ratio treatment under the 2000 growing season conditions, showed that Y decreased in the first part of the day (Figure 3) because of fruit shrinkage and generally increased after 2 pm to reach a maximum at the end of the night because of fruit swelling. These changes in Y are proportional to the rate of fruit volume change (Equation 14).

The parameter aL_f was found to be equal to $1.555\ 10^{-2} \pm 8.3\ 10^{-4}$ g cm^{-2} MPa^{-1} h^{-1}. With a ratio of the composite membrane area to the fruit area of 0.0273 (Fishman and Génard, 1998), the hydraulic conductivity of the fruit is 0.570 g cm^{-2} MPa^{-1} h^{-1}. This value is of the same order of magnitude as the hydraulic conductivity values found for maize roots - $9.72\ 10^{-2}$ g cm^{-2} MPa^{-1} h^{-1} (Steudle *et al.*, 1993) - and plant membranes - 0.2664 g cm^{-2} MPa^{-1} h^{-1} (Nobel, 1974). The product of the ratio of the composite membrane area to the fruit area and hydraulic conductivity of xylem was estimated to be $4.9\ 10^{-3} \pm 1.9\ 10^{-4}$ g cm^{-2} MPa^{-1} h^{-1}, which is about 32% of the global hydraulic conductivity of the fruit. The hydraulic conductivity of phloem is therefore more than two times greater than that of xylem, as reported for tomato (Ho *et al.*, 1987) and for grape berry, especially during the second stage of fruit development (Ollat and Gaudillère, 1996).

3.2 Test of the model

Figure 4 shows that the model accurately predicted the water growth trend of the flesh during three different periods when these estimated parameters were used. The shrinkage and the swelling of the fruit were also well simulated during the successive days of simulation.

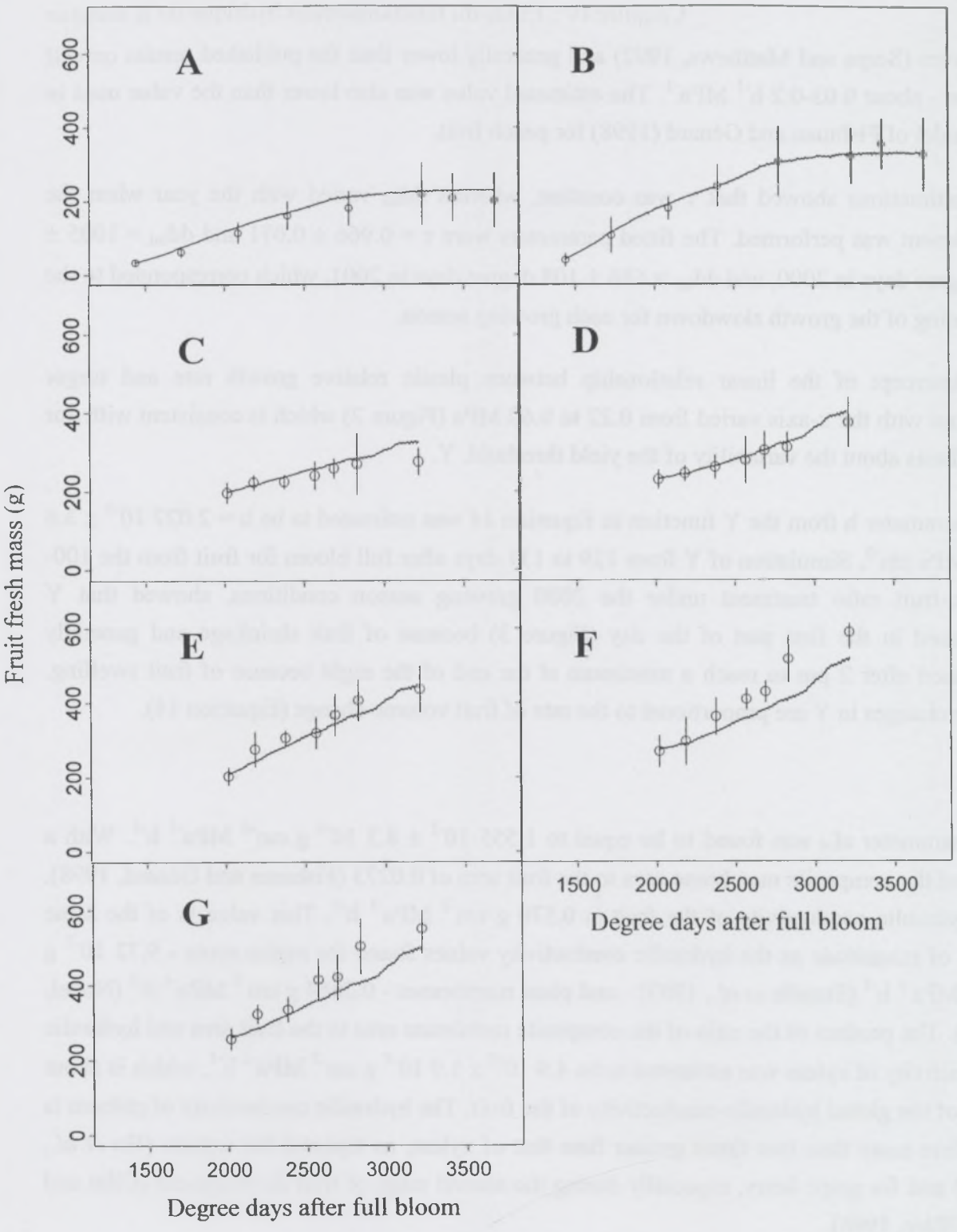

Figure 5: Comparison of simulated (curve) and measured (symbols) growth of fruit fresh mass for different girdling treatments, with the 10- and 100-leaf-to-fruit ratio treatments in 2001 (A and B) and with 10, 25, 50, 100 and 150 leaf-to-fruit ratio treatments in 2000 (C, D, E, F and G). Each point is the mean of six fruits. Vertical bars represent standard deviations of measurements.

The simulations of fresh mass variation of fruits from five leaf-to-fruit ratios in 2000 and two leaf-to-fruit ratios in 2001 correctly fitted the observations (Figure 5). The model was able to reproduce the effect of leaf-to-fruit ratio on fruit growth in fresh mass over two successive years. A weak underestimation of fruit mass from treatments with a high leaf-to-fruit ratio was observed in 2000 (Figures 5F and 5G).

Figure 6 shows the simulation of the determining variables concerning fruit water relations such as water potential and osmotic and turgor pressures for three days during the season. Simulated water potential and osmotic and turgor pressures were of the same order of magnitude as observations. The turgor pressure was well simulated except during the second period of measurement when it was underestimated (Figure 6B). The turgor pressure did not decrease to zero even during fruit shrinkage. The osmotic pressure was well predicted compared to measurements.

3.3 Analysis of model sensitivity to parameters

A sensitivity analysis was performed using the environmental conditions of the growing season in 2001 and the seasonal dry mass (input data) from 10- and 100-leaf-to-fruit ratio treatments. Sensitivity of the seasonal mean of the daily shrinkage and of the fruit growth rate to model parameters were investigated (Table 2). The shrinkage was sensitive to the fruit surface conductance, ρ. Shrinkage was also sensitive to the elasticity modulus, ε, and to the parameter, aL_f, but not to plastic parameters such as the extensibility of cell walls and h, except in the case of a 20 % decrease of dd_{ini}.

The fruit growth rate was very sensitive to parameters dd_{ini}, τ and, to a lesser extent, to h. The fruit growth rate was not sensitive to ρ, aL_f and ϕ_{max}. Before the decrease of the wall extensibility (i.e. with $dd < dd_{ini}$), the fruit growth rate was two times more affected by variations of h than when ϕ decreased (data not shown).

Shrinkage and fruit growth rates were sensitive in the same range, regardless of the leaf-to-fruit ratio.

3.4 Elastic and plastic growth rates

The model was used to analyse elastic and plastic growth rate on a diurnal basis. The simulated elastic and plastic components of the variations in fruit volume are presented on Figure 7 for periods of large and limited growth rate, between 91 and 93 DAB, and between 129 and 131 DAB, respectively, in 2000 for fruit from the 100-leaf-to-fruit ratio treatment.

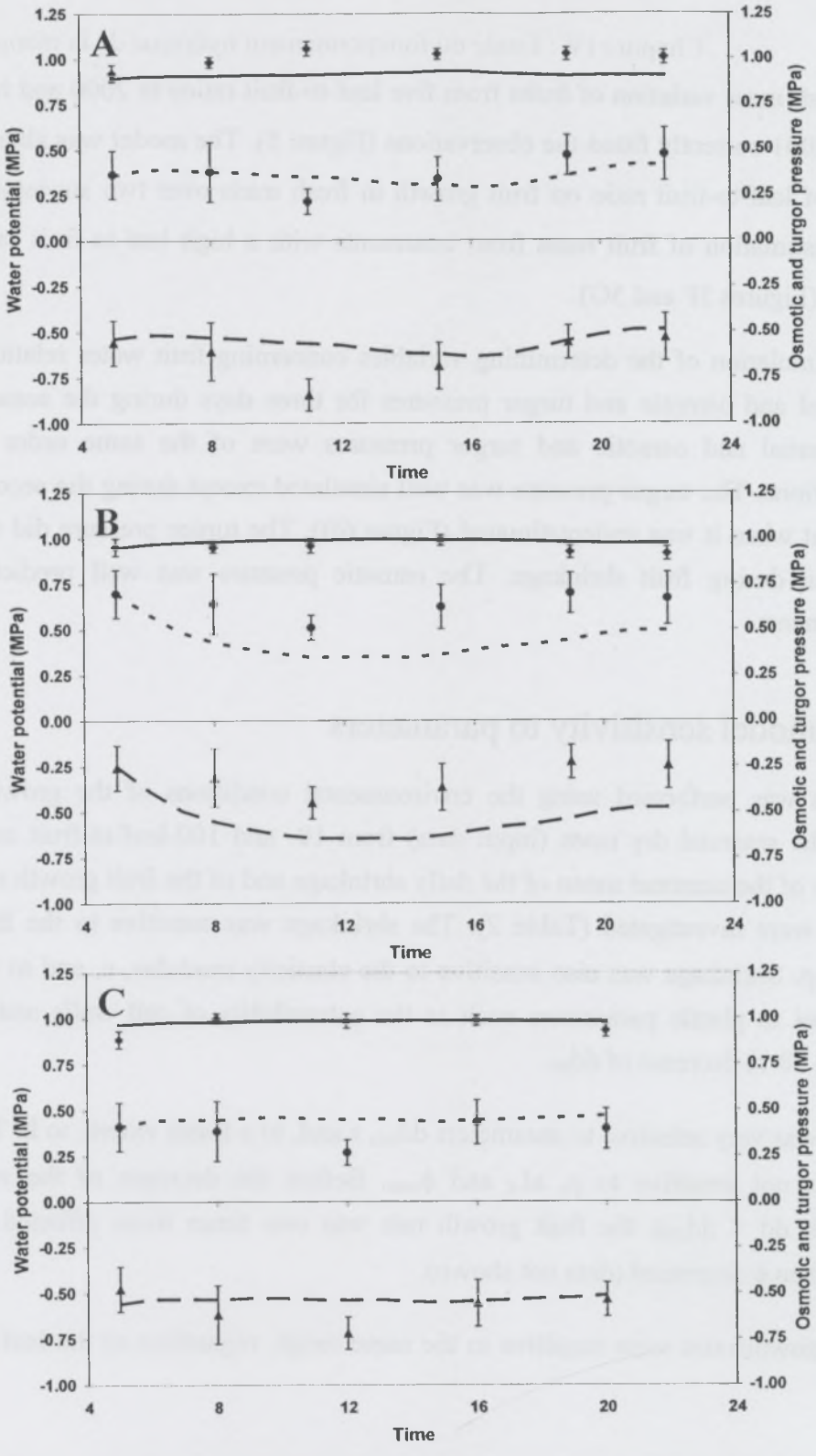

Figure 6: Diurnal variations of observed (symbols) and simulated (lines) osmotic pressure (diamond, unbroken line), turgor pressure (circle, dotted line), and water potential (triangle, broken line) in fruits from the 100-leaf-to-fruit ratio treatment over three days on the 8th (A), 25th (B) and 29th (C) November during the 2002 growing season. Vertical bars represent standard deviations of measurements.

4 Discussion

The model accurately predicted the diurnal variation of fruit water mass. The concomitant diurnal variations in fruit transpiration (maximum at midday) and in the stem water potential (minimum at midday) induced a negative fruit water balance from the morning until the mid-afternoon. Consequently, the fruit turgor pressure decreased. The model, taking into account the elastic growth, predicted positive turgor pressure even during high shrinkage, contrary to the model of Fishman and Génard (1998) which neglected the elastic deformation and predicted a null pressure in such cases. This is in accordance with our measurements and measurements made on peaches (McFadyen *et al.*, 1996) and apples (Mills *et al.*, 1997). Indeed, during the day, the plastic growth as described by the model was generally null and the shrinkage and swelling were linked to the elastic behaviour of the fruit. The plastic growth occurred mainly during the night. The elastic modulus, which reflects the elasticity of the fruit, affected the shrinkage as had already been observed on stem diameter variations (Génard *et al.*, 2001). Contrary to stem variations (Génard *et al.*, 2001), fruit shrinkage is sensitive to a parameter of water inflow, aL_f.

The rate of simulated elastic deformation probably increased during fruit growth due to the fact that this rate is directly proportional to fruit size. Observations of diurnal volume variations showed that fruit shrinkage was higher in the latter stage of fruit growth for peach (Huguet and Génard, 1995) and for mango in our experiment as well. Moreover, as fruit size increases, the yield threshold, Y, also increases, possibly decreasing the difference between fruit turgor and Y and leading to the decrease of the plastic component of fruit growth during the season.

Simulated seasonal fresh masses from two successive years were in good agreement with the measurements. Moreover, the decrease of fresh mass with decreasing leaf-to-fruit ratio was in good agreement with the observations and a previous study (Léchaudel *et al.*, 2002). However, the fruit mass from treatments with the highest leaf-to-fruit ratio in 2000 was slightly underestimated. Urban *et al.* (2002) showed that increasing the leaf-to-fruit ratio from 45 to 100 leaves per fruit on mango increased the leaf diffusive conductance to water vapour by about 45%. Leaves from trees with light crop loads have higher water potentials according to Berman and Dejong (1996). A constant stem water potential was used for the simulations, regardless of the leaf-to-fruit ratio. Increasing the stem water potential when leaf-to-fruit ratio is higher may lead to an increase in fruit water uptake and fruit mass, as a result.

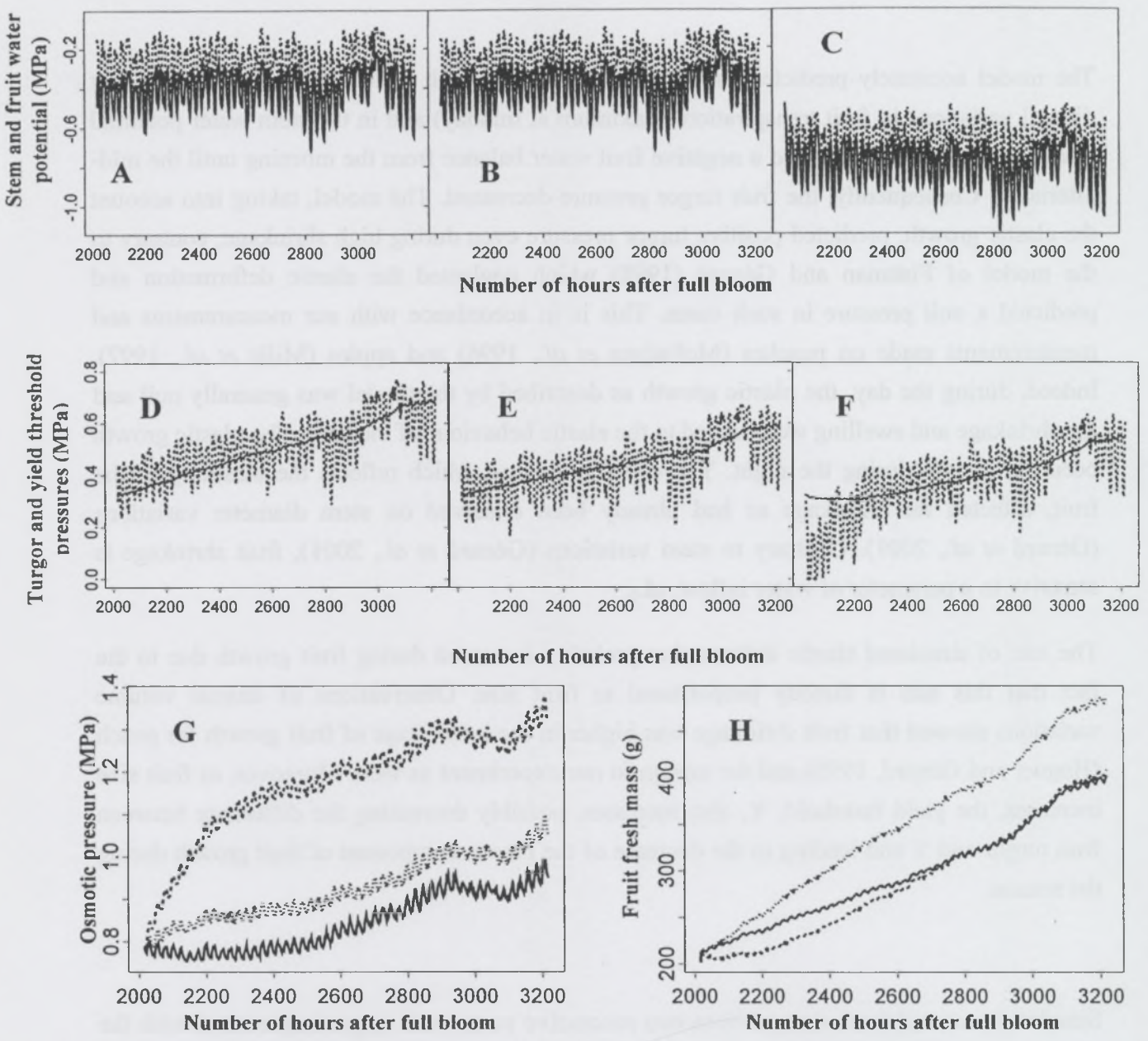

Figure 8: Effect of assimilates and water shortage on fruit water relations and fruit growth, simulated during the 2000 growing season. Stem and fruit water potentials are indicated by dotted and full lines for the control (A), the carbon stress (B) and the water stress (C) treatments, respectively. The turgor pressure and the yield threshold turgor are represented by dotted and full lines for the control (D), the carbon stress (E), and the water stress (F) treatments, respectively. Fruit osmotic potential (G) and fruit mass (H) are represented according to treatments; control (dotted line), assimilate (full line) and water (broken line) shortage.

The rate of elastic growth was negative in the morning and became positive in the afternoon. The plastic extension was positive during the night and became null after a few hours in the morning. Since the plastic fruit growth is null during the day, the fruit volume variation only depends on the elastic behaviour of the fruit. During the period of limited growth rate, the plastic component of fruit growth was lower and the elastic component of fruit growth was two times higher than during the period of large growth rate (Figure 7B). However, regardless of the period of fruit growth, the sum of the rate of elastic deformation over a day was close to zero. As a consequence, the sum of elastic deformation over the growing season was less than 2% of the total fruit growth.

3.5 Effect of assimilate or water supply shortage on fruit water relations and composition

The model was run for a 'control' fruit, and two fruits undergoing a continuous shortage in assimilate or water supply, respectively. The 'control' fruit corresponded to a fruit growing on a stem with 150 leaves, with a stem water potential in the range of well-watering treatment. A leaf-to-fruit ratio of 25 and a stem water potential of 0.40 MPa lower than the control were imposed. During the season, the shortage of water and carbon supply led to a final fruit mass equal to 80% of the final fruit mass of the control (Figure 8H). This carbon or water stress had various effects on fruit water relations (Figure 8) and fruit composition (Figure 9). For the water stress treatment, the fruit growth was almost totally stopped for a few days following the water shortage (Figure 8H). This null fruit growth was the result of a turgor pressure under the yield threshold, Y (Figure 8F). Since the dry matter inflow was maintained and water inflow was decreased after that time, the osmotic pressure increased sharply. The fruit osmotic pressure shifted 0.5 MPa forward compared to the control, but the variations around the trend were quite similar (Figure 8G). The shift in osmotic pressure increased the water inflow to the fruit and led to turgor pressure over the yield threshold, inducing a resumption of growth. For the carbon supply treatment, fruit growth slowed down compared to the control, due to a lower dry matter inflow that decreased the osmotic pressure (Figure 8G) and the turgor pressure as well (Figure 8E), whereas fruit water potential was similar (Figure 8B).

The fruit composition varied considerably according to the kind of stress (Figure 9). Thus, at maturity, total soluble sugar and mineral concentrations were higher in fruits from water stress treatment. Differences in acid concentration were found during growth but none were observed at maturity.

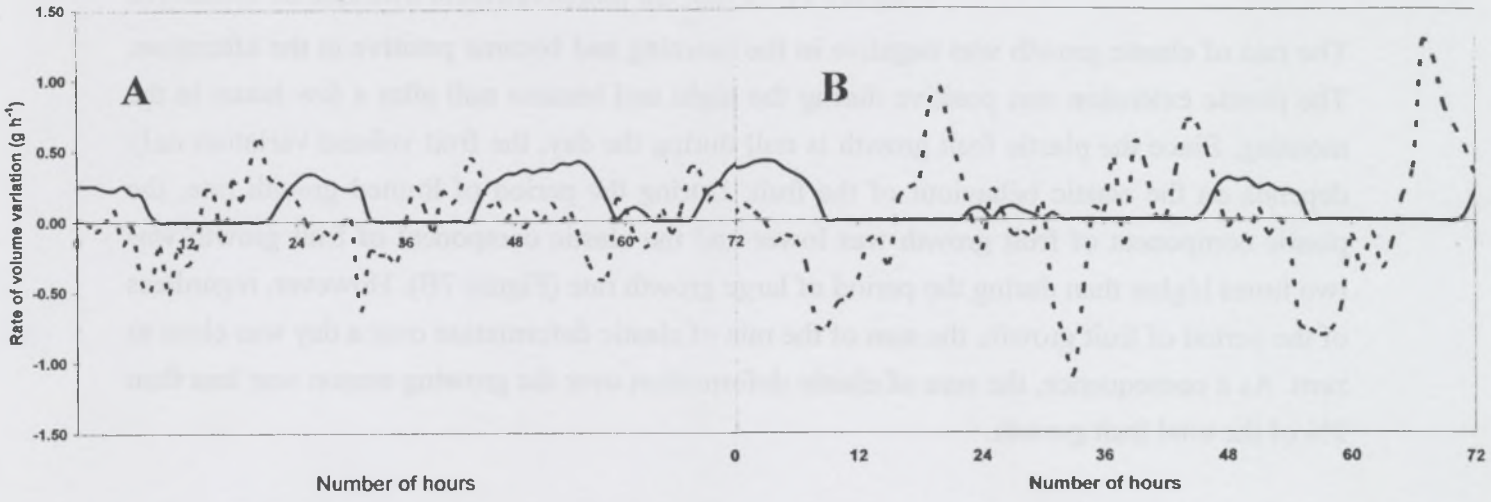

Figure 7: Simulated elastic (broken line) and plastic (full line) components of the flesh volume variations for periods of large and limited growth rate, between 91 and 93 DAB (A), and between 129 and 131 DAB (B), respectively, in 2000 for fruit from the 100-leaf-to-fruit ratio treatment.

Table 2: Sensitivity of the mean daily shrinkage on the growing season and the fruit growth rate after ± 20% variation of the model parameters.

Values are expressed as a percentage of the reference condition. The simulations used for the calculation of the mean daily shrinkage on the growing season and the fruit growth rate were performed on fruits from the 10- and 100-leaf-to-fruit ratio treatments during the 2001 growing season.

Parameter and Level of Variation (%)	Shrinkage		Fruit Growth Rate	
Leaf to fruit ratio	10	100	10	100
Water inflow and transpiration				
aL_f +20	+6	+6	+2	+2
-20	-8	-8	-3	-2
ρ +20	+8	+8	-1	-1
-20	-8	-8	+1	+1
Elastic extension				
ε +20	-10	-10	0	0
-20	+13	+12	0	0
Plastic extension				
ϕ +20	+2	+2	+1	+1
-20	-2	-2	-2	-1
dd_{ini} +20	+1	+1	+21	+18
-20	-8	-7	-21	-19
τ +20	-4	-5	+46	+38
-20	-2	-1	-7	-7
h +20	-4	-5	-5	-5
-20	+4	+5	+6	+6

Our simulations indicated that lower leaf-to-fruit ratio did not change fruit water potential but decreased fruit osmotic pressure instead. Similar relationships between crop load and fruit osmotic pressure have already been observed on peach fruit (McFadyen *et al.*, 1996). The lower osmotic pressure in fruits under high crop load was due to the decrease in concentration of osmotically-active compounds, especially acids during the first part of fruit growth, and total soluble sugars near maturity. In peach fruit, the concentrations of sucrose, the main soluble sugar in the flesh near maturity, and citrate, the major acid in the first part of fruit growth, also decreased significantly with the number of leaves per fruit (Génard *et al.*, 2003; Wu *et al.*, 2002). Since the fruit water potential was not modified with crop load, the higher simulated osmotic pressure for light crop load induced a higher turgor pressure, increasing the plastic growth and, therefore, increasing the fruit fresh mass.

The response of fruit growth and composition to reduced plant water status has been extensively studied in order to minimise water use. Fruit water relations were analysed to evaluate this response on apple (Mills *et al.*, 1996), pear (Behboudian *et al.*, 1994) and citrus (Huang *et al.*, 2000) fruit. In our study, simulated fruit growth was reduced when water stress was applied, mainly due to the lower stem water potential and the lower fruit turgor pressure, as reported in previous studies. In this case, a strong increase in osmotic pressure then occurred, as has often been measured during water stress (Huang *et al.*, 2000; Mills *et al.*, 1997; Yakushiji *et al.*, 1998), and resulted in an increase of fruit turgor. Acid concentration was the main component of osmotic potential affected by water stress. The acidity of Satsuma mandarin fruit was significantly higher after drought stress (Yakushiji *et al.*, 1998). The total sugar content was twice as high in Satsuma mandarin fruit after drought stress than in control fruit (Yakushiji *et al.*, 1998). Mills *et al.* (1997) noted that malic acid significantly contributed to the difference in osmotic potential between irrigated and early deficit irrigated treatments on apple fruit. The higher concentration of total soluble sugars simulated in our case of water stress was in accordance with experiments on apple fruit which clearly show the contribution of glucose and fructose to the increase of the osmotic potential (Mills *et al.*, 1997). Even if final fruit size of carbon and water stress treatments were close to each other, an increase in total soluble sugar and mineral concentrations at maturity were simulated from water stress treatment, while acids were degraded and not affected during this period. This may be beneficial to the internal quality of these fruits.

Fruit growth rate was highly sensitive to variations of the parameters involved in the evolution of cell wall extensibility (i.e. dd_{ini} and τ), as well as the threshold value Y (i.e. h parameter). It has already been reported that the growth rate of stem diameter (Génard *et al.*, 2001) and the growth of peach fruit (Fishman and Génard, 1998) were sensitive to Y. The

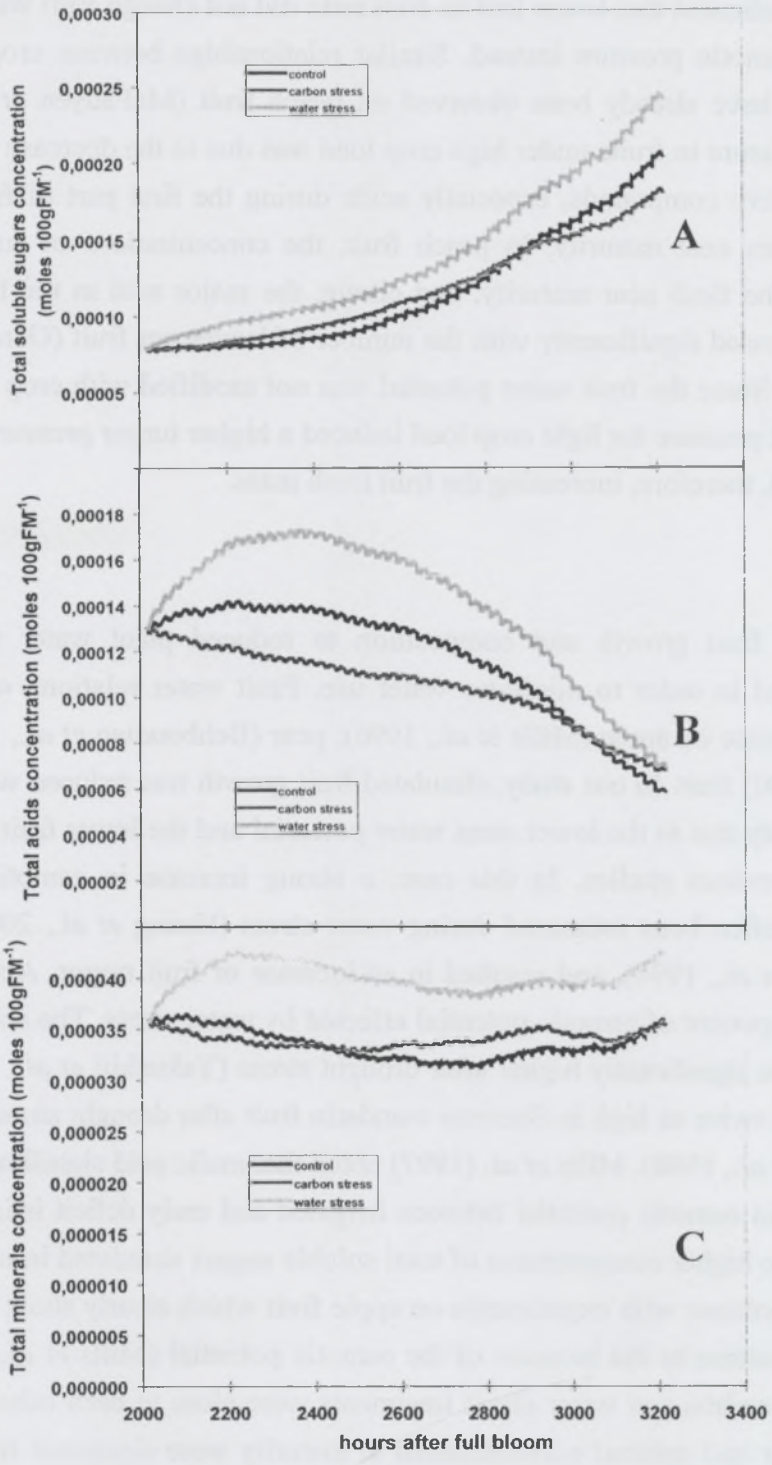

Figure 9: Effect of assimilates and water shortage on total soluble sugar (A), total acid (B), and total mineral (C) concentrations simulated during the 2000 growing season.

relationship between turgor pressure versus fruit volume variations established in our experiment revealed that parameter Y is certainly variable. Y is a parameter which may change rapidly, as demonstrated by Green *et al.* (1971) in *Nitella*. In the absence of metabolic softening (this means that parameter s is equal to zero as assumed here), Y changes with the fruit growth rate. When fruit turgor pressure decreases, the fruit growth and, therefore, Y are reduced, which makes it possible to maintain growth at low turgor pressure. The possibility of a rapid adjustment in the yield threshold in response to changes in growth rate was shown by Frensch and Hsiao (1995) after osmotic stress on maize roots. A similar change in Y was reported in an intact seedling of soybean (Maruyama and Boyer, 1994). To illustrate the dynamics of the yield threshold pressure, *in vitro* studies have demonstrated an acid-induced decrease in the yield threshold tension (y) in the cell wall of hypocotyl segments (Okamoto and Okamoto, 1994). Hormonal and pH controls of Y will have to be considered in detail in order to further develop the model. To promote elongation, the auxin-induced acidification of the apoplast changes the mechanical properties of the cell wall. These properties are controlled by functional proteins which were isolated as yieldin wall-bound proteins (Okamoto-Nakazato *et al.*, 2000).

The other main parameter which regulates fruit growth, cell wall extensibility, is also affected by auxin-induced acidification (Okamoto and Okamoto, 1994).By analysing wall metabolism, Huang *et al.* (2000) showed a wall adjustment mechanism affecting the cell wall extensibility of fruit under water stress conditions. Some wall-bound proteins like expansins are able to disrupt the hydrogen bonds that connect the cellulose microfibrils and the hemicelluloses in the cell wall (McQueen-Mason, 1995). McQueen-Mason (1995) used a cucumber hypocotyl to demonstrate that as cells mature, expansin activity is reduced and the wall is modified. Cell wall enzymes such as xyloglucan endotransglycosidase (XET) and specific peroxidases (Thompson *et al.*, 1998) are involved in the regulation of cell wall extensibility. This alteration in wall structure regulates the cessation of growth. Analysing the correlation between cell wall enzyme activities and tomato fruit growth, Thompson *et al.* (1998) proposed that the rate of fruit growth may be determined by epidermal XET activity, and the end of growth by the rise of peroxydase activity. In our model, fruit growth is partly regulated by changes in cell wall extensibility. This variable was constant during the early development and then decreased. The role of pH was not directly introduced, even if the pH of the mango flesh increases at the end of fruit growth, which may be related to the decrease in cell wall extensibility. Cell wall extensibility began to decrease at different times, depending on the year. The pH may be a source of this variation. Studies of fruit pH during successive years often reported an inter-annual variability of this variable, as in the case of peach (Lobit, 1999). It would be interesting to determine the link between changes in pH and the decrease in wall extensibility through molecular studies that would isolate the main enzymes and their various activities during fruit growth.

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Chapitre V : Modélisation de l'élaboration de la qualité de la mangue

Chapitre V : Modélisation de l'élaboration de la qualité de la mangue

1 Introduction

Dans ce dernier chapitre, les connaissances acquises sur le fonctionnement de la mangue sont intégrées dans un modèle global qui permet de simuler l'élaboration de la qualité de la mangue au cours de son développement. L'utilisation de ce modèle comme outil de prédiction de la qualité du fruit rejoint la démarche plus appliquée de mon travail de thèse sur la maîtrise de la qualité du fruit au champ par des techniques culturales comme l'éclaircissage du fruit, la taille de formation de l'arbre, ou l'irrigation qui détermine l'éclairement intercepté par le rameau, la disponibilité carbonée et hydrique.

Les modèles utilisés pour construire ce modèle global sont le modèle de croissance en matière sèche du fruit au niveau du rameau fructifère (Chapitre III), le modèle d'évolution de la composition biochimique et minérale du fruit (Chapitre IV), et le modèle de fonctionnement hydrique du fruit (Chapitre IV). Des simplifications sont apportées au modèle de fonctionnement hydrique, en particulier le module d'élasticité est supprimé car la somme des variations de volume dues à la croissance élastique du fruit est nulle sur la saison (Chapitre IV). La suppression de la croissance élastique nécessite la modification des équations de calcul de la pression de turgescence et des variations de volume du fruit. Le modèle global de qualité du fruit fonctionne au pas de temps de la journée, excepté pour la photosynthèse foliaire. Une valeur moyenne journalière de chaque variable d'état est simulée.

L'objectif de ce modèle global est l'étude par simulation de la variation de la qualité à la récolte selon les conditions de croissance, le profil de qualité comprenant la masse fraîche du fruit, la teneur en matière sèche de la pulpe et les concentrations des principaux sucres, acides et éléments minéraux. Les concentrations simulées en sucres et en acides permettent de calculer la saveur sucrée et acide du fruit.

Le modèle global de qualité du fruit au niveau du rameau fructifère a été testé en comparant la croissance en matière fraîche simulée et observée pour différents jeux de données acquis pendant les trois années d'expérimentations dans des conditions où la disponibilité en assimilats carbonés était variable. Ce modèle a été également testé en confrontant des données obtenues sur l'évolution des saveurs sucrée et acide au cours de la saison, et sur la qualité de la mangue à la récolte (calibre, concentrations en éléments minéraux, acides et sucres) avec les simulations correspondantes.

L'analyse de sensibilité du modèle de fonctionnement carboné et l'étude virtuelle de la contribution de facteurs influençant les processus impliqués dans la croissance ont montré que la masse initiale est un facteur explicatif important de la croissance en matière sèche. Par

ailleurs, la date de récolte est connue de longue date par les producteurs comme un levier de maîtrise de la qualité. Le modèle global a donc été utilisé, dans les mêmes conditions d'alimentation carbonée, pour analyser les effets de la masse initiale et de la date de récolte sur la croissance, l'état hydrique du fruit et sur les principaux critères de qualité simulés par ce modèle.

2 Matériel et méthodes

2.1 Description des modifications apportées aux modèles utilisés

Le modèle de croissance en matière sèche du fruit est utilisé dans sa version présentée dans le Chapitre III. Il permet de simuler la photosynthèse foliaire, les respirations d'entretien des différents compartiments et de croissance du fruit, la demande du fruit, et la remobilisation des réserves, qui interviennent au cours de la croissance en matière sèche du fruit. La matière sèche du fruit accumulée chaque jour est séparée entre le noyau et le reste du fruit à partir des relations allométriques décrites dans le Chapitre II entre la masse sèche de chaque compartiment (peau, pulpe, noyau) et la masses sèche du fruit.

Le modèle du fonctionnement hydrique du fruit est modifié principalement au niveau du calcul de la pression de turgescence et des variations en volume de la pulpe qui ne tiennent plus compte des variations élastiques du fruit.

Les variations de volume de la pulpe (V) sont liées au flux d'eau entrant (U), aux pertes par transpiration (T), et également à l'accumulation d'eau $\left(\frac{dw}{dt}\right)$ et de matière sèche $\left(\frac{d(DM)}{dt}\right)$:

$$\frac{dV}{dt} = \frac{1}{D_w} \cdot \frac{dw}{dt} + \frac{1}{D_s} \cdot \frac{d(DM)}{dt} = \frac{1}{D_w} \cdot (U - T) + \frac{1}{D_s} \cdot \frac{d(DM)}{dt} \quad (1)$$

avec D_w et D_s les densités de l'eau et de la matière sèche, respectivement égales à 1 et à 1.6.

Les flux d'eau entrant et sortant du fruit sont calculés de la même manière que pour le modèle de fonctionnement hydrique du fruit (Chapitre IV).

Les variations de volume de la pulpe sont liées à la croissance irréversible par l'équation de Lockhart (1965) :

$$\frac{dV}{dt} = \phi \cdot V \cdot (P_f - Y) \qquad if\ P_f > Y \tag{2}$$

$$\frac{dV}{dt} = 0 \qquad if\ P_f \leq Y \tag{3}$$

avec P_f, la pression de turgescence, ϕ (MPa^{-1} j^{-1}) l'extensibilité des parois, Y (MPa) la pression seuil au-dessus de laquelle la croissance est irréversible.

Combinant les Equations 1, 2, et 3, la pression de turgescence du fruit est calculée de la manière suivante :

$$P_f = \frac{\dfrac{\phi \cdot V \cdot Y + A_f \cdot aL_f \cdot (\Psi_s + \pi_f) - T}{D_w} + \dfrac{1}{D_s} \cdot \dfrac{ds}{dt}}{V \cdot \phi + A_f \cdot aL_f} \qquad if\ (P_f \geq Y) \tag{4}$$

$$P_f = \frac{(\Psi_s + \pi_f)}{D_w} + \frac{(-T) + \dfrac{1}{D_s} \cdot \dfrac{ds}{dt}}{A_f \cdot aL_f} \qquad if\ (P_f < Y) \tag{5}$$

avec, aL_f = 0.3732 g cm^{-2} MPa^{-1} j^{-1}, le produit du rapport de la surface de la membrane composite, qui sépare les vaisseaux conducteurs des cellules, sur la surface du fruit, et de la conductivité hydraulique du fruit, paramètre défini au Chapitre IV.

Y et ϕ suivent les mêmes lois de variation que dans le modèle horaire de fonctionnement hydrique du fruit (Chapitre IV), leurs unités respectives étant modifiées selon les cas :

$$\frac{dY}{dt} = h \cdot \frac{dV}{dt} \tag{6}$$

avec h (MPa cm^{-3}), d'où $Y(t) = h \cdot V(t)$.

et pour l'extensibilité des parois :

$$\phi = \phi_{max} \qquad if\ dd < dd_{ini}$$

$$\phi = \phi_{max} \cdot \tau^{(dd - dd_{ini})} \qquad if\ dd > dd_{ini} \tag{7}$$

Tableau 1: Paramètres du modèle global d'élaboration de la qualité de la mangue.

Parameter	Equation	Value
	Carbon assimilation by leaves	
p_1 (µmol CO_2 m^{-2} s^{-1} g^{-1})	Eq. 1 (Chap. III)	3.85 ± 0.57
p_2 (µmol CO_2 m^{-2} s^{-1})	Eq. 1 (Chap. III)	33.23 ± 11.91
p_3 (dimensionless)	Eq. 1 (Chap. III, App. 2)	0.483 ± 0.074
p_4 (dimensionless)	Eq. 1 (Chap. III, App. 2)	0.034 ± 0.007
	Maintenance respiration	
MRR_{leaves} (g carbon g^{-1} $hour^{-1}$)	Eq. 3 (Chap. III, App. 2)	$1.56\ 10^{-4}$
MRR_{stem} (g carbon g^{-1} day^{-1})	Eq. 3 (Chap. III, App. 2)	$8.58\ 10^{-4}$
MRR_{fruit} (g carbon g^{-1} day^{-1})	Eq. 6 (Chap. III)	$1.15\ 10^{-3} \pm 1.1\ 10^{-4}$
Q_{10}^{leaves} (dimensionless)	Eq. 3 (Chap. III, App. 2)	2.11
Q_{10}^{stem} (dimensionless)	Eq. 3 (Chap. III, App. 2)	1.96
Q_{10}^{fruit} (dimensionless)	Eq. 3 (Chap. III, App. 2)	1.90
	Potential fruit growth	
RGR_{ini} (dd^{-1})	Eq. 2 (Chap. III)	0.0105 ± 0.0003
a (dimensionless)	Eq. 3 (Chap. III)	16.736 ± 1.637
b (dimensionless)	Eq. 3 (Chap. III)	0.624 ± 0.036
GRC_{fruit} (g carbon g^{-1})	Eq. 6 et 7 (Chap. III)	0.04 ± 0.01
c_{fruit} (g carbon g^{-1})	Eq. 7 (Chap. III)	0.4239 ± 0.0048
	Reserve mobilisation	
r_4	Eq. 5 (Chap. III, App. 2)	0.0162
r_5	Eq. 6 (Chap. III, App. 2)	0.0164
	Transpiration	
ρ (cm h^{-1})	Eq. 2 (Chap. IV)	231.0 ± 5.9
Hf (dimensionless)	Eq. 2 (Chap. IV)	0.996
γ (dimensionless) η (dimensionless)	Eq. 3 (Chap. IV)	3.65 ± 0.21 0.73 ± 0.10
	Plastic fruit growth	
a.L (g cm^{-2} MPa^{-1} j^{-1})	Eq. 4 et 5 (Chap. V)	0.3732
h (MPa g^{-1})	Eq. 6 (Chap. V)	2.027 10-3 ± 3.6 10-5
ϕ_{max} (MPa^{-1} j^{-1})	Eq. 7 (Chap. V)	0.414
τ	Eq. 7 (Chap. V)	0.966 ± 0.071
a_{ini}	Eq. 8 (Chap. V)	20.77
b_{ini}	Eq. 8 (Chap. V)	518.87

avec ϕ_{max} = 0.414 MPa^{-1} $jour^{-1}$, τ ayant la même valeur que dans le modèle de croissance de fonctionnement hydrique du fruit.

Le paramètre dd_{ini} a été estimé variable en fonction des années. A partir des valeurs estimées en 2000 et 2001 (Chapitre IV), la relation empirique suivante est proposée pour calculer ce paramètre en fonction de la masse initiale du fruit (DM_f^{ini}) :

$$dd_{ini} = a_{ini} \cdot DM_f^{ini} + b_{ini} \quad (8)$$

Nous faisons l'hypothèse que dans un fruit petit au stade "initial", supposé constitué d'un faible nombre de cellules, le ralentissement de la croissance et la maturation auraient lieu tôt à cause d'un remplissage plus rapide des cellules.

Les variables d'état, comme la transpiration, la pression osmotique et de turgescence, sont calculées chaque jour. La quantité d'eau accumulée par jour dans la chair est additionnée à la masse sèche de la chair. Pour obtenir les variations de masse fraîche du fruit, la masse fraîche du noyau est calculé grâce aux relations allométriques présentées dans le Chapitre II, qui relient la masse sèche du noyau à la masse sèche sec du fruit, et la masse d'eau du noyau à sa masse sèche.

Les saveurs sucrée (CSu) et acide (CAc) du fruit sont calculées de la manière suivante :

$$SSu = \sum_i cs_i \cdot X_i \,, \quad (9)$$

et $$SAc = \sum_j ca_j \cdot X_j \quad (10)$$

avec cs_i le pouvoir sucrant du sucre i et X_i sa concentration (g $100gMF^{-1}$), ca_j, le pouvoir acidifiant de l'acide j et X_j sa concentration (g $100gMF^{-1}$). L'amidon est une forme de stockage qui n'intervient pas dans la saveur sucrée du fruit. Selon Kulp *et al.* (1991) le fructose et le glucose ont un pouvoir sucrant de 1.75 et 0.77 g de saccharose / g respectivement. A acidité titrable et pH donnés, l'acide citrique est perçu comme moins acide que l'acide malique (Noble *et al.*, 1986). Le pouvoir acidifiant de l'acide malique serait de 1.33 g d'acide citrique / g (Fabian and Blum, 1943).

La définition et la valeur des paramètres utilisés dans le modèle global de croissance en matière fraîche sont rappelées dans le Tableau 1.

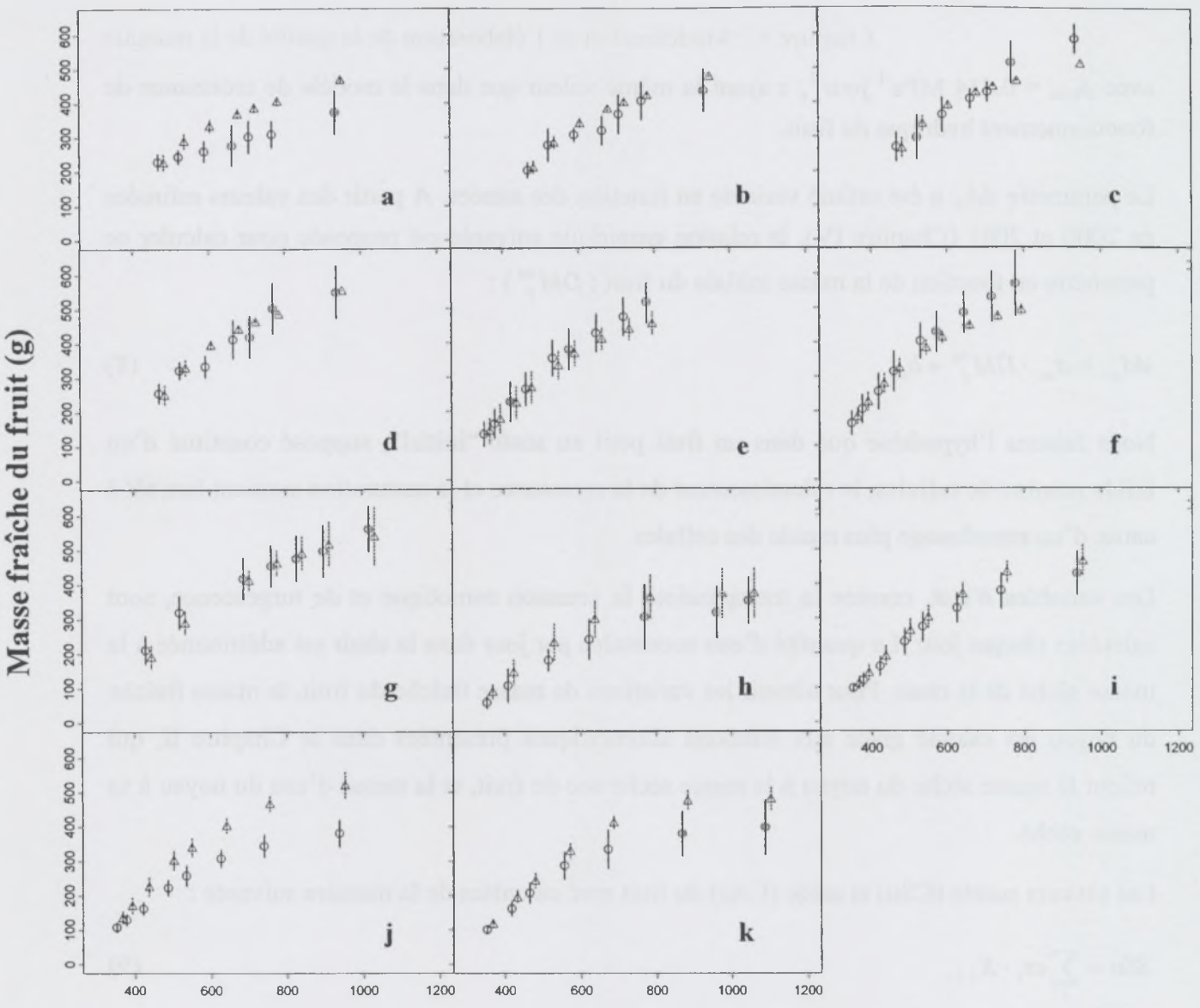

Figure 1: Comparaison du poids frais observé et simulé par le modèle pour des données utilisées pour l'estimation de paramètres ou la calibration du modèle. Ces données de croissance du fruit proviennent de mesures 'destructives' acquises à partir de la première floraison de 2000 pour les traitements 25 (a), 50 (b), 100 (c) et 150 (d), de mesures 'non destructives' acquises à partir de la première floraison de 2000 pour les traitements 100 (e) et 150 (f), de mesures 'non destructives' acquises à partir de la deuxième floraison de 2000 pour le traitement 100 (g), de mesures 'destructives' acquises à partir de la floraison de 2001 pour le traitement 100 (h), et de mesures 'non destructives' acquises à partir de la première floraison de 2002 pour le traitement 100 sur le verger 1 (i), le verger 2 (j) et de la deuxième floraison sur le verger 2 (k). La moyenne et l'écart type observés (cercle et ligne pleine) et simulés (triangle et tirets) ont été représentés sur le graphique.

2.2 Matériel végétal

L'étude a été réalisée sur les parcelles 1 et 2 du verger d'expérimentation de Bassin Plat, décrites dans le Chapitre I "Matériels et Méthodes". Les différents traitements en rapports feuilles/fruit (10, 25, 50, 100, et 150 feuilles par fruit) ont été mis en place selon les règles présentées dans le Chapitre I "Matériels et Méthodes".

2.3 Mesures de croissance et de qualité

Nous avons utilisé les jeux de données de masses fraîches de fruit, acquis au cours des trois années d'expérimentation, obtenus soit par un suivi 'non destructif' du diamètre du fruit, soit par un suivi 'destructif' de la masse fraîche du fruit (Chapitre I "Matériels et Méthodes"). Les fruits récoltés au cours des mesures 'destructives' ont été pesés, puis un échantillon de chaque fruit a été congelé de manière à analyser sa composition biochimique, selon le protocole décrit dans la partie II du Chapitre II.

2.4 Description de l'étude virtuelle concernant l'effet de la masse initiale et de la date de récolte sur la croissance et les critères de qualité à la récolte

Nous avons réalisé des simulations avec les données climatiques de la saison de croissance correspondant à la première floraison de l'année 2000. Le rapport feuilles/fruit utilisé était de 50 feuilles par fruit, ce qui est proche du rapport optimal choisi par les producteurs. Les masses sèches initiales du fruit étaient de 7 et 21 g à 350 degrés jours. Ces valeurs représentent respectivement un faible et un fort niveau de masse initiale qui correspondent à 0.5 et 2 fois la moyenne observée. Nous avons choisi comme date de récolte 900 et 1100 degrés jours (équivaut à une différence de 20 jours). Ces deux dates correspondent aux deux pics de récolte généralement observés sur une parcelle (Jannoyer and Lauri, 2002a; Jannoyer and Lauri, 2002b) entre lesquels les arboriculteurs vont réaliser des passages successifs pour récolter les mangues. Les effets de la masse initiale et de la date de récolte sur la croissance, les variables d'état liées à l'état hydrique du fruit, comme les pressions osmotique et de turgescence, et les critères de qualité a la récolte ont été analysés.

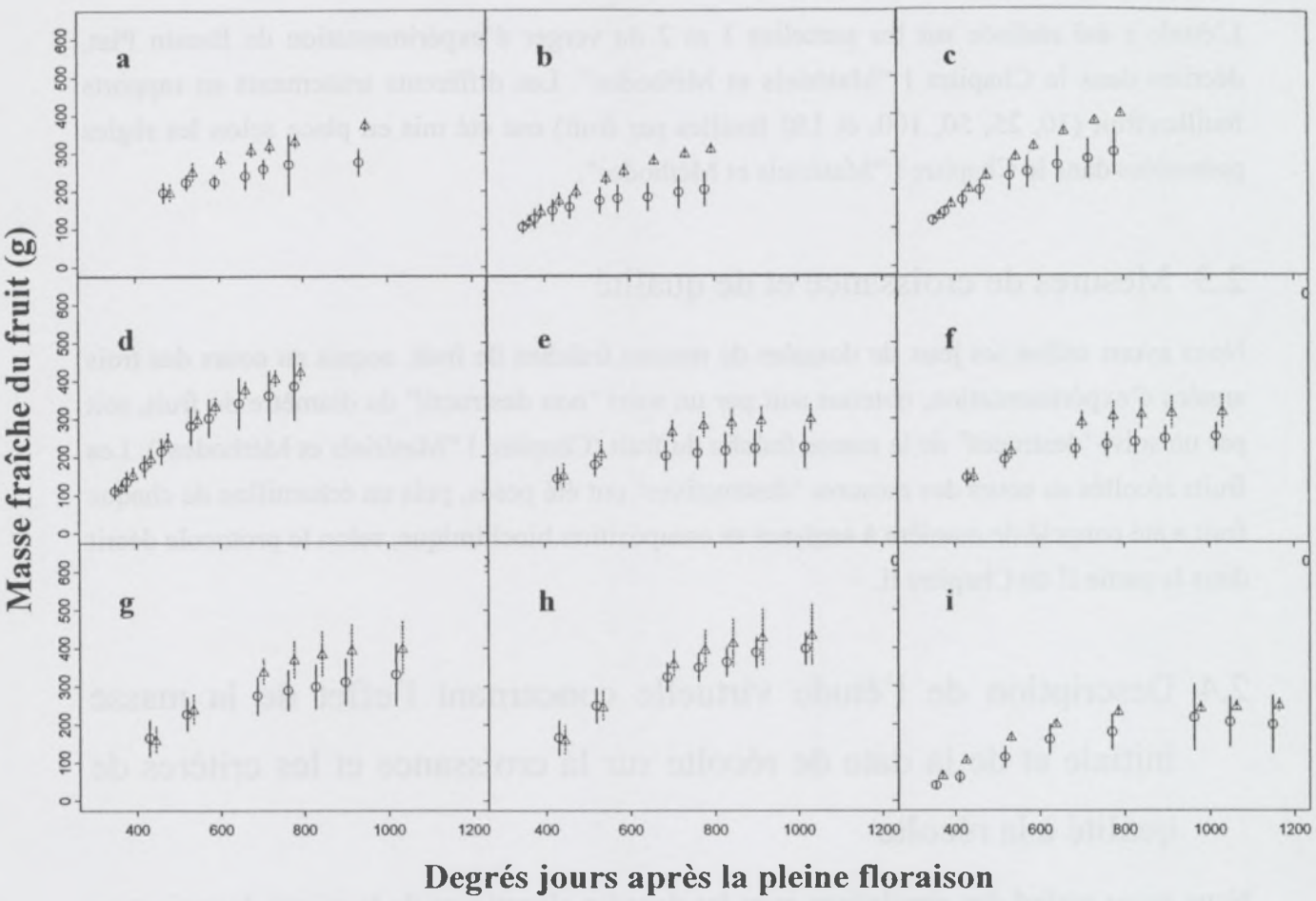

Figure 2: Comparaison du poids frais observé et simulé par le modèle pour des données indépendantes. Ces données de croissance du fruit proviennent de mesures 'destructives' acquises à partir de la première floraison de 2000 pour les traitements 10 (a), de mesures 'non destructives' acquises à partir de la première floraison de 2000 pour les traitements 10 (b), 25 (c) et 50 (d), de mesures 'non destructives' acquises à partir de la deuxième floraison de 2000 pour les traitements 10 (e), 25 (f), 50 (g) et 75 (h), et de mesures 'destructives' acquises à partir de la floraison de 2001 pour le traitement 10 (i). La moyenne et l'écart type observés (cercle et ligne pleine) et simulés (triangle et tirets) ont été représentés sur le graphique.

3 Résultats

3.1 Test du modèle

Le modèle a été testé à partir des jeux de données acquis pendant les trois années d'expérimentations. Les données climatiques (température, humidité journalières et rayonnement horaire) et les valeurs initiales utilisées pour le modèle de croissance en matière sèche du fruit permettent de faire fonctionner le modèle global. Pour représenter la variabilité de la masse fraîche du fruit observée par traitement, les simulations ont été réalisées pour chaque fruit avec leur masse sèche initiale (mesurée à 350 degrés jours). Dans les expérimentations destructives, uniquement les masses sèches des fruits récoltés à 350 degrés jours ont été utilisées pour les simulations. Pour tester la qualité prédite à la récolte, les simulations ont été effectuées en utilisant la moyenne des masses initiales disponibles dans le jeu de données testé.

Le modèle présenté précédemment décrit bien la croissance en matière fraîche de fruits se développant dans des conditions de disponibilité carbonée contrastées. L'augmentation de la masse fraîche du fruit avec le rapport feuilles/fruit est bien simulée par le modèle. La dynamique simulée de la masse fraîche du fruit chez le manguier représente bien, durant les trois années successives d'expérimentation et pour différentes floraisons au sein d'une même année, les observations acquises qui ont servi à estimer les paramètres des modèles (Figure 1) et les observations qui proviennent de jeux de données indépendants (Figure 2). En 2000, les masses fraîches des fruits des traitements 10 et 25 feuilles par fruit (Figures 1a, 2a, 2b, 2c, 2e et 2f) ont tendance à être surestimés quelque soit le type d'expérimentation (destructive ou non). Toutefois cette surestimation de la croissance des traitements avec un faible rapport feuilles/fruit est moins marquée en 2001 (Figure 2i). En 2002, les masses fraîches simulées des fruits de la parcelle 2, provenant de la première floraison, sont supérieures aux mesures (Figure 1j). La variabilité de la masse fraîche du fruit n'est pas toujours bien représentée par le modèle qui a tendance à la sous-estimer dans certaines simulations.

Les sorties du modèle concernant les critères de qualité à la récolte comme la masse fraîche, les concentrations des principaux acides organiques, sucres et éléments minéraux sont présentées dans le Tableau 2. Globalement, le modèle simule bien l'ordre de grandeur des critères de qualité à la récolte. La valeur des critères de qualité simulée à la récolte est très souvent comprise dans l'intervalle représenté par la moyenne plus ou moins l'écart type des données. L'effet fort du nombre de feuilles par fruit sur la masse fraîche est représenté par le modèle. Les concentrations observées et simulées en acides organiques ne sont pas très

Table 2 : Critères de qualité à la récolte

			poids frais		teneur en matière sèche		acide citrique		acide malique	
année	traitement	nb fruits	observé	simulé	observé	simulé	observé	simulé	observé	simulé
2000	25	5	373,21 ± 63,82	425,53	17,54 ± 3,62	17,19	1,017 ± 0,100	1,270		
	50	5	436,40 ± 62,50	436,10	18,54 ± 2,21	17,47	0,877 ± 0,141	1,258		
	100	5	587,20 ± 43,60	477,10	20,47 ± 0,83	18,38	1,076 ± 0,182	1,256		
2001	10	7	199,69 ± 75,03	246,58	18,23 ± 2,52	15,25	0,540 ± 0,286	0,744	0,322 ± 0,022	0,183
	100	7	321,85 ± 100,19	375,17	21,89 ± 1,70	14,02	0,547 ± 0,196	0,409	0,301 ± 0,014	0,219
2002	10	3	218,38 ± 76,73	253,28	15,55 ± 2,77	11,93	1,779 ± 0,610	1,009	0,154 ± 0,069	0,132
	100	3	420,17 ± 79,64	473,39	16,55 ± 0,66	14,67	1,451 ± 0,188	1,232	0,214 ± 0,013	0,024

			glucose		fructose		saccharose		amidon	
année	traitement	nb fruits	observé	simulé	observé	simulé	observé	simulé	observé	simulé
2000	25	5	0,151 ± 0,041	0,294	1,711 ± 0,198	1,334	1,932 ± 0,615	3,808	4,820 ± 1,536	4,173
	50	5	0,206 ± 0,045	0,292	1,845 ± 0,151	1,309	2,842 ± 0,572	3,831	4,136 ± 1,231	4,176
	100	5	0,216 ± 0,143	0,297	1,629 ± 0,262	1,194	2,861 ± 0,687	4,368	5,728 ± 1,621	4,562
2001	10	7	0,426 ± 0,107	0,195	2,311 ± 0,336	1,995	6,974 ± 1,021	4,260	2,443 ± 2,634	3,298
	100	7	0,467 ± 0,190	0,210	2,097 ± 0,145	1,651	7,910 ± 1,042	4,491	1,800 ± 1,483	2,286
2002	10	3	0,170 ± 0,149	0,223	1,334 ± 0,092	1,415	3,601 ± 2,412	2,403	4,267 ± 1,422	2,817
	100	3	0,241 ± 0,042	0,257	1,822 ± 0,283	1,156	6,500 ± 0,861	2,989	1,567 ± 1,553	3,826

			potassium		magnésium		calcium	
année	traitement	nb fruits	observé	simulé	observé	simulé	observé	simulé
2000	25	5	0,1408 ± 0,0161	0,1160	0,0067 ± 0,0019	0,0057	0,0110 ± 0,0021	0,0082
	50	5	0,1471 ± 0,0159	0,1150	0,0066 ± 0,0004	0,0057	0,0110 ± 0,0011	0,0080
	100	5	0,1608 ± 0,0199	0,1160	0,0074 ± 0,0013	0,0058	0,0106 ± 0,0040	0,0068
2001	10	7	0,1544 ± 0,0184	0,1278	0,0070 ± 0,0011	0,0052	0,0098 ± 0,0031	0,0104
	100	7	0,1819 ± 0,0351	0,1214	0,0089 ± 0,0021	0,0054	0,0133 ± 0,0034	0,0086
2002	10	3	0,1746 ±0,0455	0,0978	0,0096± 0,0031	0,0045	0,0103 ± 0,0029	0,0091
	100	3	0,1772 ±0,0141	0,0981	0,0116 ± 0,0020	0,0048	0,0088 ± 0,0015	0,0073

différentes selon les traitements. L'augmentation de la concentration en saccharose avec le nombre de feuilles par fruit observée à la récolte est prédite par le modèle. Toutefois, la concentration en saccharose est sous estimée en 2001 et 2002 et sur estimée en 2000. Le modèle prédit assez mal la tendance observée d'une augmentation de la concentration en magnésium et d'une faible diminution de la concentration en calcium dans les fruits des traitements avec un fort nombre de feuilles par fruit. Le modèle ne représente pas bien l'augmentation de la concentration en potassium avec le rapport feuilles/fruit.

Le modèle global simule l'augmentation de la saveur sucrée et la diminution de la saveur acide observée au cours de la croissance. Toutefois, la dynamique de la saveur sucrée et acide n'est pas toujours bien représentée chaque année. En 2002, la saveur acide est sous-estimée (Figure 3d). En 2001 pour les deux traitements 10 et 100 feuilles par fruit (Figure 3a) et en 2002 pour le traitement 100 feuilles par fruit (Figure 3c), la saveur sucrée à la fin de la croissance a tendance à être sous estimée.

3.2 Analyse par simulation de l'effet de la masse initiale et de la date de récolte

La masse fraîche d'un fruit virtuel ayant une masse initiale plus élevée est plus importante que celle d'un fruit ayant une plus faible masse initiale, tout au long de la saison de croissance (Figure 4a). Cette différence entre les deux courbes de croissance simulées augmente avec les degrés jours (Figure 4a), elle est de 90 g à 350 degrés jours et de plus de 200 g à la récolte à 1100 degrés jours. On observe durant la majeure partie de la saison que les pressions osmotique et de turgescence du gros fruit virtuel, qui a une masse initiale de 21 g, sont supérieures, d'environ 0,2 MPa, à celles du petit fruit qui a une masse initiale de 7 g (Figure 4b). Toutefois, le seuil de pression au dessus duquel la croissance est irréversible est plus important dans le gros fruit (Figure 4b), ce qui indique que pour ce fruit la différence entre la pression de turgescence et Y n'est pas obligatoirement supérieure à celle dans le petit fruit. Entre 800 et 1100 degrés jours, la différence entre la pression de turgescence et Y s'accentue dans le petit fruit (Figure 4b) sans une augmentation de croissance, due à la diminution de l'extensibilité des parois plus précoce que pour me gros fruit. La Figure 4c montre l'évolution de la vitesse de croissance calculée par l'équation de Lockhart (1965). La vitesse de croissance du gros fruit virtuel est positive la majeure partie de la saison. Cette vitesse est nulle après 800 degrés jours pour le petit fruit virtuel. Au début des simulations, la vitesse de croissance du gros fruit virtuel est supérieure à celle du petit fruit, alors qu'entre 500 et 700 degrés jours, la vitesse de croissance du gros fruit est inférieure. Entre 700 et 1100 degrés jours, la vitesse de croissance simulée du gros fruit virtuel est supérieure ou égale à celle du petit fruit.

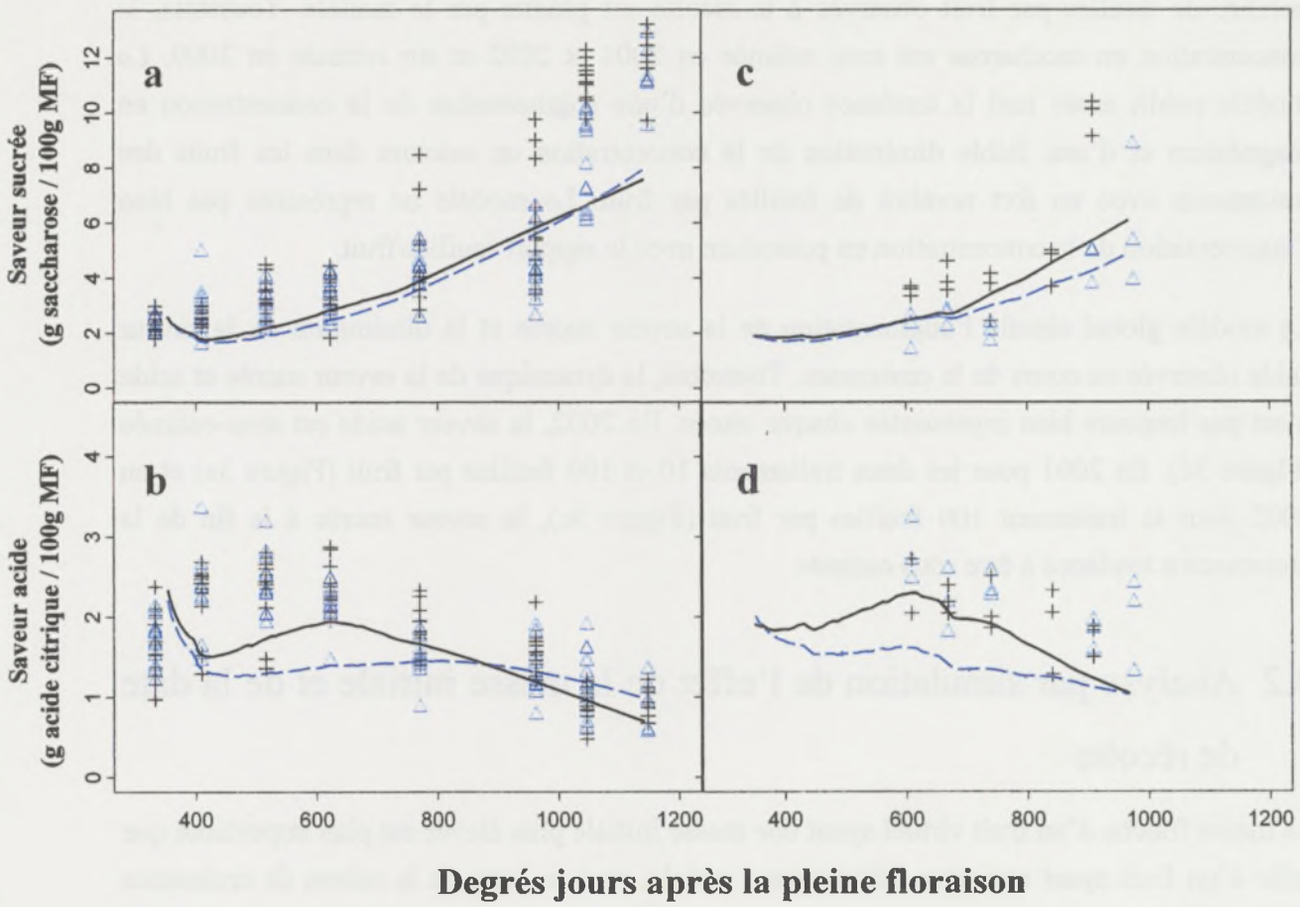

Figure 3: Comparaison des saveurs sucrée et acide observée (symboles) et simulée (lignes) en 2001 (a et b) et 2002 (c et d) pour les traitements 10 (triangle et ligne discontinue) et 100 (croix et ligne continue) feuilles par fruit.

Les effets de la masse initiale et de la date de récolte sur les critères de qualité à la récolte sont présentés dans le Tableau 3. La masse fraîche du fruit et la teneur en matière sèche à la récolte augmentent avec la masse initiale. En considérant la même date de récolte, le gros fruit virtuel a une saveur sucrée plus forte que le petit fruit, avec une différence un peu moins marqué à 900 degrés jours. A 900 degrés jours, la saveur acide n'est pas affectée par la masse initiale du fruit. A 1100 degrés jours, le gros fruit virtuel a une saveur acide plus faible que le petit fruit, ce qui peut s'expliquer par une concentration en acide citrique plus faible dans le gros fruit. Faire varier la masse initiale ne modifie pas significativement les concentrations en glucose et magnésium. La concentration en fructose est plus élevée dans les petits fruits. Les concentrations en saccharose (à 900 et 1100 degrés jours) et potassium (à 1100 degrés jours) augmentent avec la masse initiale. La concentration en calcium est légèrement supérieure dans le fruit virtuel ayant la masse initiale de 7 g.

La masse fraîche du fruit qui a une masse initiale élevée a augmenté entre 900 et 1100 degrés jours, alors que celui qui a une faible masse initiale a peu évolué. La teneur en matière sèche des fruits quelques soit la masse initiale n'a pas augmenté entre les récoltes à 900 et 1100 degrés jours. Par contre la saveur sucrée a augmenté, ainsi que les concentrations en saccharose et fructose, alors que celle en amidon a diminué. La saveur acide et conjointement les concentrations en acide citrique ont diminué entre ces deux dates de récoltes. Les concentrations en éléments minéraux ne sont pas affectées par la date de récolte, sauf la concentration en potassium qui a tendance à augmenter avec la date de récolte.

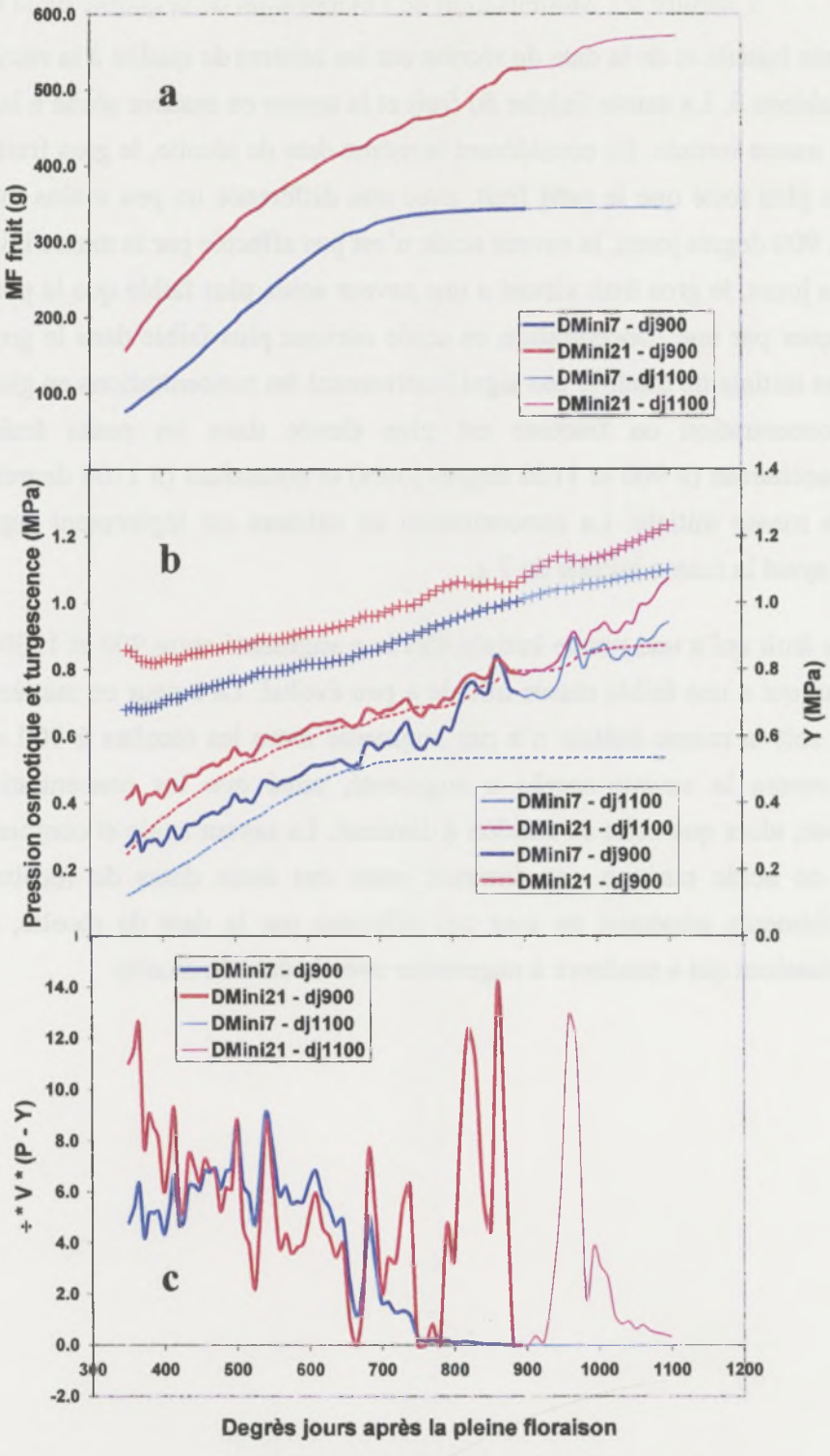

Figure 4: Effets de la masse initiale ("DMini") et de la date de récolte ("dj") sur la croissance en matière fraîche (a), l'état hydrique du fruit (b) et la vitesse de croissance irréversible (c). En (b), deux composantes de l'état hydrique du fruit, les pressions osmotiques (+) et de turgescence (ligne), et la variable Y (pointillés) sont analysées.

4 Discussion

Le modèle d'élaboration de la qualité du fruit au niveau du rameau est capable de représenter l'évolution de la croissance en matière fraîche du fruit mesurée au cours des trois années d'expérimentation et également les variations de croissance selon les niveaux de rapports feuilles/fruit. La surestimation par le modèle de la masse fraîche des fruits des traitements avec un faible rapport feuilles/fruit peut être due aux variations du potentiel hydrique de tige en fonction du rapport feuilles/fruit qui ne sont pas prises en compte dans le modèle. En effet, Urban *et al.* (2002) ont montré chez le manguier que la diminution du rapport feuilles/fruit de 100 à 25 entraînait une augmentation de 45 % de la conductance stomatique des feuilles. Du fait de cette capacité transpiratoire plus importante, le potentiel hydrique de tige devrait être plus faible pour les faibles rapports feuilles/fruit. Les observations de McFadyen *et al.* (1996) sur le pêcher en forte et faible charge vont dans ce sens. Pour améliorer nos simulations, il faudrait établir chez le manguier la loi de variation du potentiel hydrique de tige en fonction du rapport feuilles/fruit.

La variation de la croissance en matière fraîche au sein d'un même traitement n'est pas toujours bien décrite et elle est souvent inférieure à la variation observée. On peut expliquer cela, d'une part, par le fait que pour les simulations on a considéré dans chaque cas un éclairement "moyen" du rameau (valeur d'entrée), négligeant ainsi la variabilité réelle de l'environnement lumineux. Cela a pu minimiser la variabilité simulée de la masse sèche du fruit par rapport à la variabilité réelle (Chapitre III). D'autre part, lors du calcul de la transpiration du fruit, nous avons choisi par soucis de simplicité de prendre un coefficient de perméabilité de la peau du fruit à l'eau constant. Or, il apparaît chez certaines espèces que ce coefficient varie au cours de la croissance (Lescourret *et al.*, 2001), en raison notamment des modifications de la structure et donc de l'épaisseur de la cuticule ; cas de la pêche (Crisosto *et al.*, 1994); cas de la cerise (Knoche *et al.*, 2001), ou de l'apparition de microcraquelures au niveau du péricarpe ; cas du letchi par exemple (Huang *et al.*, 1999). La prise en compte dans notre modèle de la variabilité de la perméabilité de la cuticule entre fruits est donc une voie intéressante à explorer.

La cinétique des concentrations en sucres solubles et acides organiques n'est pas toujours bien représentée par le modèle, ce qui affecte la qualité de l'estimation de la cinétique des saveurs sucrée et acide. Toutefois, les critères de qualité à la récolte, comme la masse fraîche, la teneur en matière sèche et les concentrations des principaux sucres, acides et éléments minéraux sont globalement bien estimées. La teneur en matière sèche du fruit est sous estimée

Table 3 : Analyse virtuelle de l'effet de la masse initiale et de la date de récolte sur les critères de qualité à la récolte, le poids frais, le teneur en matière sèche de la pulpe, la saveur sucrée, la saveur acide et les concentrations (g / g matière fraîche) en acides, sucres et minéraux dans la pulpe.

Masse initiale	Date de récolte	Poids frais (g)	Teneur en matière sèche (%)	Saveur sucrée	Saveur acide
7 g	900	342,77	0,14	5,12	1,41
7 g	1100	344,19	0,14	7,12	0,87
21 g	900	527,67	0,18	5,75	1,41
21 g	1100	570,79	0,17	9,12	0,45

Masse initiale	Date de récolte	Acide malique	Acide citrique	Glucose	Fructose	Saccharose	Amidon	potassium	magnésium	calcium
7 g	900	0,10	1,28	0,27	1,35	2,55	3,45	0,104	0,005	0,009
7 g	1100	0,19	0,61	0,22	1,64	4,08	2,65	0,118	0,005	0,009
21 g	900	0,00	1,41	0,27	1,02	3,75	4,97	0,100	0,005	0,006
21 g	1100	0,34	0,00	0,33	1,26	6,66	0,94	0,146	0,008	0,007

en 2001 du fait de la sous-estimation de la masse sèche du fruit (Chapitre III) et de la légère surestimation de la masse fraîche.

Les différences entre les concentrations observées et simulées des différents composés sont en particulier dues à l'utilisation du modèle empirique qui a été établi sur l'année d'expérimentation 2001, et dont les capacité prédictives sont faibles comme c'est souvent le cas pour ce type de modèle (Marcelis *et al.*, 1998). De plus, la comparaison de concentrations par gramme de masse fraîche est toujours délicate. Les concentrations sont un rapport entre des quantités d'un élément et la masse fraîche du fruit. De petites erreurs sur les quantités et sur la masse peuvent se traduire par une erreur importante de leur rapport, c'est-à-dire la concentration. Nous avons également observé que le modèle empirique de composition de la pulpe est très sensible à la matière sèche de la pulpe, une erreur sur cette variable peut avoir des conséquences importantes sur les concentrations simulées.

Ces résultats sur la composition biochimique de la mangue indiquent qu'il serait intéressant d'utiliser des approches plus mécanistes pour simuler l'élaboration de la qualité, comme celle qui est proposée sur la pêche pour modéliser l'accumulation des sucres (Génard *et al.*, 2003; Génard and Souty, 1996) et des acides organiques (Lobit *et al.*, 2003).

Dans le Chapitre III, nous avons vu que la masse initiale influençait fortement la croissance en matière sèche de la mangue. Les résultats de l'étude virtuelle montrent que la croissance en matière fraîche du fruit est également plus importante quand la masse initiale est forte. Dans ce cas, la pression osmotique a augmenté ce qui est probablement dû à l'augmentation des concentrations en sucres, lesquels représentent les principaux composés osmotiquement actifs du fruit. Cette augmentation de la pression osmotique est contrebalancée par une augmentation de la pression de turgescence ce qui induit une augmentation plus forte de la croissance en matière fraîche des fruits, comme l'ont montré McFadyen *et al.* (1996) en étudiant le lien entre les relations hydriques dans le fruit et sa croissance.

Le fruit virtuel qui a une masse initiale élevée a une vitesse de croissance plus importante que celui qui a une faible masse initiale en cas de récolte tardive. Ce fruit est plus sucré et moins acide, ce qui est en accord avec la relation entre la vitesse de croissance et la qualité gustative du fruit observée chez la pêche (Génard *et al.*, 1991). La diminution des concentrations en acides pour les fruits ayant une plus grosse masse initiale et récoltés plus tard a été également mis en évidence chez la pomme (Sullivan, 1965). En comparant des variétés de mangue, Mukerjee (1959) a observé que la variété Dashehari qui est caractérisée par son petit calibre accumule plus de sucres réducteurs que de sucres non réducteurs. Les plus fortes

concentrations en fructose simulées dans les fruits ayant une masse initiale de 7 g sont en accord avec ces résultats.

L'effet de la masse initiale sur la conservation du fruit peut être pris en compte dans les résultats de l'étude virtuelle. Les travaux de Simmons *et al.* (1998) et Hofman *et al.* (1995) indiquent que des teneurs en matière sèche plus fortes et des concentrations en calcium plus faibles, observées dans notre étude virtuelle pour les fruits ayant une plus grosse masse initiale, s'accompagnent d'une réduction de la durée de conservation des fruits.

La croissance du fruit virtuel qui a une faible masse initiale n'a pas évolué entre 900 et 1100 degrés jours, alors que les concentrations en saccharose et fructose ont augmenté et celle en amidon a diminué. Ces résultats indiquent que les processus impliqués dans la maturation devaient avoir lieu à 900 degrés jours dans le petit fruit virtuel, ce qui est cohérent avec les travaux sur la diminution de l'extensibilité des parois quand la croissance ralentit et que les cellules deviennent matures (McQueen-Mason, 1995; Thompson *et al.*, 1998). Cet effet est moins marqué avec le gros fruit virtuel dont la masse fraîche augmente encore de 8 % entre 900 et 1100 degrés jours, ce qui indique que ce fruit accumule encore des assimilats carbonés. La très faible concentration en amidon à la date de récolte la plus tardive indique que dans ce fruit la maturation est bien avancée à cette date (Mendoza and Wills, 1984; Tandon and Kalra, 1983).

L'augmentation de la saveur sucrée avec l'éloignement de la date de récolte est surtout liée chez la mangue à l'augmentation de la concentration en fructose et saccharose comme l'ont observé Tandon and Kalra (1983) pour le cultivar 'Dashehari'. L'augmentation de la concentration en saccharose et la diminution de la concentration en amidon avec la date de récolte indiquent que les fruits récoltés plus tard ont logiquement un stade de maturation plus avancé et une meilleure qualité à la récolte. Toutefois, ces fruits récoltés plus tard devraient avoir une qualité gustative après conservation plus faible (Volz *et al.*, 1995).

Ces résultats montrent que le modèle proposé simule au moins qualitativement les changements dans la composition de la mangue qui ont lieu en fin de croissance et qui conditionnent sa qualité organoleptique. Le processus de maturation doit y participer fortement et pourrait être influencé par des facteurs comme la masse initiale. Cet aspect serait à étudier dans de futures recherches.

Les modèles décrivant le fonctionnement carboné (Chapitre III) et hydrique (Chapitre IV) du fruit nous ont permis de construire un modèle de croissance en matière fraîche du fruit et de prédiction de la qualité à la récolte. Ce modèle est capable de décrire avec une bonne précision l'évolution de la croissance en matière fraîche du fruit dans des conditions

contrastées d'alimentation carbonée. La prédiction de la dynamique des concentrations des principaux composés biochimiques liés à la qualité du fruit n'est pas toujours très bonne, néanmoins la prédiction de ces critères de qualité à une date de récolte proche de la pleine maturité est acceptable. De plus, l'étude virtuelle réalisée à partir de ce modèle a montré que l'effet de la masse initiale du fruit sur la croissance en matière fraîche était de plus en plus marqué à mesure que le fruit se développe et pouvait s'expliquer par un effet sur les composantes de l'état hydrique du fruit. La masse initiale affecte également la qualité des fruits à la récolte en améliorant des critères de qualité gustative, mais en réduisant des indicateurs de la durée de conservation du fruit, comme la teneur en matière sèche et la concentration en calcium. Cette étude virtuelle a confirmé qu'une date de récolte tardive permet d'améliorer des critères liés à la qualité gustative du fruit. Toutefois, retarder la date de récolte ne permet un gain en masse fraîche que pour les fruits ayant une masse initiale élevée.

Conclusions et perspectives

Conclusions et perspectives

1 Bilan des connaissances acquises

L'approche descriptive (Chapitre II) a montré l'importance de la liaison entre l'accumulation du carbone et de l'eau dans les différents compartiments de la mangue (peau, pulpe, noyau). Au cours du développement du fruit, dans chaque compartiment, la vitesse d'accumulation de l'eau ralentit alors que celle de la matière sèche augmente. Ceci est fortement marqué dans le noyau dont la deuxième partie du développement se distingue par la phase de durcissement (Saini *et al.*, 1971). Le noyau est le compartiment dont les coûts de construction des tissus sont les plus importants, suivi de la peau puis de la pulpe (Chapitre III). Des variations du rapport feuilles/fruit modifient la compartimentation du carbone, mais également celle de l'eau. A la récolte, les fruits du traitement 100 feuilles/fruit ont ainsi une part plus importante de leur masse fraîche comprise dans la pulpe, en comparaison avec les fruits des traitements avec un plus faible rapport feuilles/fruit. Cette observation est intéressante d'un point de vue pratique, la pulpe étant le compartiment qui intéresse le plus les consommateurs.

L'approche descriptive concernant l'effet de la disponibilité carbonée et hydrique sur l'élaboration de la qualité de la mangue a tout d'abord confirmé que la masse fraîche du fruit était fortement affectée par des variations du rapport feuilles/fruit. Nous avons choisi dans cette approche de décomposer la concentration par gramme de matière fraîche des principaux composés présents dans la pulpe de mangue par le produit de la teneur en matière sèche, de la teneur en matière sèche structurale, et de la concentration par gramme de matière sèche structurale de chaque composé. Les effets des facteurs agronomiques sur chacune des trois composantes sont les suivant :

- la teneur en matière sèche augmente avec le rapport feuille/fruit.

- la teneur en matière sèche structurale qui représente la proportion de parois par masse sèche de fruit, n'est pas affectée par les facteurs agronomiques.

- les concentrations des différents composés exprimées par gramme de masse sèche structurale sont positivement (saccharose), négativement (acides citrique et malique, calcium et fructose) ou ne sont pas affectées (potassium, magnésium et glucose) par une augmentation de la disponibilité carbonée.

Les expérimentations sur le fonctionnement carboné de la mangue ont permis de construire et de valider un modèle de croissance en matière sèche du fruit qui prend en compte l'effet du

climat, de facteurs internes à la plante et des facteurs agronomiques sur les relations sources/puits. Ce modèle fonctionne bien pour la période de croissance comprise entre la mesure de la masse initiale du fruit (environ 350 degrés jours après la pleine floraison) et la maturité.

Le modèle n'est pas sensible aux paramètres liés à la respiration d'entretien du système, à la respiration de croissance du fruit et à la mobilisation des réserves des feuilles et du rameau. Par contre, le modèle est très sensible aux paramètres de la photosynthèse foliaire et à la demande du fruit.

Une étude virtuelle nous a permis de quantifier les contributions respectives du climat, de la masse initiale du fruit et du rapport feuilles/fruit pour les processus physiologiques impliqués dans la croissance, en particulier la photosynthèse et la demande du fruit. Nous avons vu que la contribution du climat est globalement inférieure à celles des autres facteurs modifiant les relations sources/puits. Le rapport feuilles/fruit contribue fortement à la variation de la photosynthèse foliaire. La forte contribution de la masse initiale du fruit, considéré comme un indicateur du nombre de cellules, dans sa demande et plus généralement dans sa croissance, montre que la mangue s'inscrit dans un schéma de fonctionnement où le développement précoce du fruit conditionne la masse finale du fruit. Ce schéma a été mis en évidence chez d'autres espèces comme la tomate (Ho, 1984) et la banane (Jullien, 2000).

Les expérimentations sur le fonctionnement hydrique de la mangue nous ont permis de construire un modèle qui intègre les propriétés d'élasticité et de plasticité des parois des cellules de la pulpe, ce qui n'a jamais été fait à notre connaissance au niveau du fruit. Ce modèle simule des pressions de turgescence qui sont du même ordre de grandeur que les pressions que nous avons mesurées sur des tissus de pulpe et celles obtenues sur pêches (McFadyen *et al.*, 1996) et pommes (Mills *et al.*, 1997). Une originalité dans ce travail d'intégration vient de l'introduction dans ce modèle des variables Y (le seuil de pression de turgescence au dessus duquel la croissance est irréversible) et ϕ (la plasticité des parois) pour la croissance plastique (Lockhart, 1965), et d'un paramètre ε (le module d'élasticité) pour la croissance élastique (Ortega, 1985). Les variables Y et ϕ suivent des lois de variation dont l'expression générale provient d'expérimentations au niveau cellulaire et tissulaire (Bütenmeyer *et al.*, 1998; Green *et al.*, 1971; Proseus *et al.*, 1999). Ces lois de variation ont ensuite été ajustées pour la mangue. Le modèle validé au pas de temps horaire permet de séparer la croissance plastique, irréversible, de la croissance élastique, réversible.

Une étude virtuelle utilisant ce modèle de fonctionnement hydrique du fruit a été effectuée pour analyser et comparer les effets d'une variation de la disponibilité carbonée d'une part et hydrique d'autre part sur la croissance et les relations hydriques du fruit. Les résultats des

simulations sont en accord avec les observations fournies par la littérature. Ce dispositif virtuel montre qu'il est possible à partir de ce modèle, testé dans des conditions d'alimentation carbonée variables, d'étudier et de comprendre les effets d'autres facteurs, tel que l'alimentation hydrique, sur la croissance du fruit.

Des limites apparaissent dans cette étude du fonctionnement hydrique de la mangue. Le choix d'introduire un module d'élasticité constant peut être remis en question, car des travaux ont mis en évidence que le module d'élasticité serait fonction du volume des cellules (Jones *et al.*, 1985; Steudle and Wieneke, 1985) et de la pression de turgescence (Ortega, 1990; Tyree and Jarvis, 1982). Il peut être envisagé d'appliquer des méthodes de déformation des tissus pour mesurer la déformation élastique de ces tissus (Milad and Shackel, 1992) et de réaliser une étude plus approfondie du module d'élasticité chez la mangue.

Les modèles décrivant le fonctionnement carboné (Chapitre III) et hydrique (Chapitre IV) du fruit nous ont permis de construire un modèle de croissance en matière fraîche du fruit et de prédiction de la qualité à la récolte. Nous avons vu dans le Chapitre V que la prédiction de la dynamique des concentrations des principaux composés biochimiques liés à la qualité du fruit n'est pas toujours très bonne, néanmoins les valeurs des critères de qualité simulés à la récolte sont acceptables.

L'étude virtuelle réalisée à partir de ce modèle global a montré que l'effet de la masse initiale du fruit sur la croissance en matière fraîche était de plus en plus marquée au fur et à mesure du développement du fruit et pouvait s'expliquer par un effet sur les composantes de l'état hydrique du fruit. De plus, l'augmentation de la masse initiale du fruit a tendance à améliorer des critères de qualité gustative, comme la saveur sucrée, les concentrations en sucres et acides, mais à affecter des indicateurs de la durée de conservation du fruit, comme la teneur en matière sèche et la concentration en calcium. D'un point de vue agronomique, cette étude virtuelle a mis en évidence qu'une date de récolte tardive permettant d'améliorer des critères liés à la qualité gustative du fruit ne permet un gain en masse fraîche que pour les fruits ayant une masse initiale élevée.

2 Perspectives de recherche

La question de la généralisation de la démarche présentée sur le fonctionnement d'un rameau de manguier peut être abordée à deux niveaux : soit un approfondissement de l'analyse écophysiologique, en la généralisant à la plante entière, soit une application du modèle (i) vers l'agronomie en utilisant le modèle comme un outil d'aide au pilotage de la parcelle et de prédiction de caractéristiques de récolte, (ii) vers l'analyse de la variabilité génétique de la qualité de la mangue en utilisant les paramètres du modèle comme des constantes génétiques dont on étudiera la variabilité (Quillot, 2003).

2.1 Approfondissement de l'approche écophysiologique

Si l'on fait l'hypothèse que la variabilité de la qualité dans la plante est avant tout due à celle de l'alimentation carbonée, il semble nécessaire d'une part d'approfondir certains aspects du fonctionnement du modèle de croissance en matière sèche, et d'autre part d'aborder les transferts de carbone entre rameaux. Dans l'approche originale, proposée dans la thèse, sur le fonctionnement hydrique de la mangue l'analyse et la modélisation concernant la limitation des flux d'eau arrivant dans le fruit et les relations entre l'extensibilité des parois des tissus et la physiologie du fruit seraient à affiner. L'insuffisance des résultats des simulations du modèle de prédiction de la qualité du fruit à la récolte suggère d'utiliser une approche différente pour simuler l'accumulation des sucres et des acides. Enfin le processus de maturation dont on connaît l'importance dans l'expression de la qualité, n'a pas été étudié dans le cadre de cette thèse. Des perspectives d'étude de ce processus seront proposées.

2.1.1 Echelle de l'arbre

Au niveau des sources, modéliser la distribution des assimilats carbonés est important pour prédire l'hétérogénéité de la croissance du fruit au sein d'un arbre (Grossman and Dejong, 1994; Le Roux *et al.*, 2001). Au cours du travail de thèse, nous avons utilisé un modèle simple et peu précis de la photosynthèse foliaire, qui tient compte de la demande du fruit et de l'environnement lumineux du rameau, pour déterminer la photosynthèse foliaire. Pour approfondir cet aspect, j'ai participé aux travaux de L. Urban sur le modèle biochimique de photosynthèse proposé par Farquhar *et al.* (1980), qui est fréquemment utilisé et qui relie les paramètres clés de la capacité photosynthétique des feuilles à l'azote foliaire par unité de surface, Na. Urban *et al.* (2003) ont montré chez le manguier que la capacité photosynthétique de feuilles proches de fruit était supérieure à celle des autres feuilles. Ma participation à ces

travaux se concentre sur la partie concernant l'effet du rapport feuilles/fruit sur les paramètres clés de la capacité photosynthétique et sur Na. Ce travail a été décrit dans quatre articles, dont deux sont parus (Urban, L., Bertheuil, F. and Léchaudel, M. 2002. A coupled photosynthesis and stomatal conductance model for mango leaves. *Acta Horticulturae*. 584 : 81-88 et Urban, L., Léchaudel, M. and Lu, P. 2003. Phenological effects on photosynthesis: suggestions for modelling. *In Plant Growth Modeling and Applications*, Bao-Gang Hu & M. Jaeger Eds. Proceedings-PMA03, Beijing, China, October 13-16. p. 67-75), un soumis (Urban, L. and Léchaudel, M. Effect of leaf-to-fruit ratio on leaf nitrogen content and net photosynthesis in girdled branches of mango. Manuscript soumis à *Tree Physiology*) et un dernier en élaboration (Urban, L., Léchaudel, M. and Lu, P. Interpreting the effect of fruit load on leaf photosynthesis in girdled branches of mango. Manuscript à envoyer à *Journal of Experimental Botany*). Ces articles reprennent le modèle biochimique de la photosynthèse foliaire chez le manguier, présentent nos résultats concernant l'effet du rapport feuilles/fruit sur le contenu en azote et la photosynthèse des feuilles et sur les paramètres clés de la capacité photosynthétique. Les perspectives sont de prendre explicitement en compte l'effet de la disponibilité carbonée sur la capacité photosynthétique en affinant la relation obtenue entre les sucres totaux contenus dans les feuilles et Na, et d'intégrer ce modèle biochimique de photosynthèse au modèle de fonctionnement carboné du rameau que nous avons proposé.

La variabilité de la croissance des fruits au niveau de l'arbre est peu documentée, les modèles existants regroupant l'ensemble des fruits au sein d'un même compartiment (Buwalda, 1991; Grossman and Dejong, 1994). Il serait intéressant de coupler notre modèle de fonctionnement carboné du rameau aux représentations du fonctionnement carboné de l'arbre proposées dans les modèles de croissance d'arbres utilisés en foresterie et en écologie (Le Roux *et al.*, 2001). Il serait possible de décrire le manguier comme une collection de rameaux qui ont un fonctionnement proche de celui modélisé par notre modèle. Les transferts de carbohydrates entre ces rameaux seraient à modéliser. Il existe de nombreuses approches pour modéliser l'allocation du carbone, comme l'utilisation de coefficients d'allocation empiriques, de schémas flux-résistances, ou des approches sources-puits (Le Roux *et al.*, 2001). Pour bien simuler l'acquisition du carbone, il est nécessaire de connaître l'environnement lumineux des rameaux. Notre approche devrait donc être couplée à une représentation de l'architecture du manguier (travail en cours dans le cadre de l'ATP manguier du CIRAD, cf Introduction) et à un modèle d'interception de la lumière par le couvert du manguier.

2.1.2 Echelle du fruit

Au niveau des puits, le modèle de fonctionnement carboné du rameau, qui prend en compte l'effet des conditions environnementales et des pratiques culturales sur les relations

sources/puits, simule correctement l'évolution de la masse sèche du fruit pour la période de croissance comprise entre la mesure de la masse initiale du fruit (350 degrés jours après la pleine floraison) et la maturité. Des travaux sur la croissance précoce sont à envisager. En effet, l'analyse de sensibilité du modèle de croissance en matière sèche et l'expérimentation virtuelle ont montré que la masse initiale contribue fortement aux processus impliqués dans la croissance du fruit. La caractérisation plus précise du stade "masse initiale" dans le développement du fruit est à effectuer, en travaillant depuis la floraison jusqu'à ce stade. Des coupes histologiques pourraient être réalisées pour définir précisément les stades de développement du fruit (phase active de division cellulaire, fin de mise en place des cellules de la pulpe, indice mitotique), comme l'a fait Jullien (2000) sur la banane. L'étude du déterminisme du nombre de cellules est à envisager. Des travaux soulignent l'importance des températures pendant les 5 à 6 semaines après la pleine floraison (Blanpied and Ben-David, 1970; Tromp, 1997). Ainsi, chez la pomme, des relations entre la température et la vitesse de division cellulaire ont été établies pour modéliser les phases précoces du développement (Austin *et al.*, 1999). Le travail initié au cours de la thèse pour relier la masse finale du fruit au nombre final de cellules peut être poursuivi, car il a donné des résultats prometteurs qui sont en accord avec les travaux menés sur d'autres fruits (Bertin *et al.*, 2002; Cowan *et al.*, 1997; Harmens *et al.*, 2000).

Lors de l'analyse du fonctionnement hydrique de la mangue, le fruit a été considéré comme une grosse cellule attachée directement au xylème. La mangue possède une longue panicule qui la rattache au rameau. La conductivité hydraulique de ces tissus pourrait-elle être limitante pour la croissance du fruit ? Chez la tomate, des travaux indiquent que les résistances dans le pédicelle du jeune fruit sont fortes, le potentiel hydrique de l'eau à l'entrée du fruit étant alors très bas (Bussières, 2002). Nous avons considéré un flux global d'eau qui entre dans le fruit par flux de masse. Une perspective de mon travail de thèse serait de séparer le flux d'eau apporté par le xylème de celui apporté par le phloème et de voir comment les conductivités hydrauliques du xylème et du phloème varient. Pour déterminer la conductivité hydraulique du xylème, il faudrait suivre les variations de croissance d'un fruit avec la panicule décortiquée (phloème détruit) pendant assez de temps pour laisser le flux xylémien se stabiliser. Notre modèle de fonctionnement hydrique nous permettrait alors d'estimer la valeur de la conductivité hydraulique du xylème. A partir des variations de croissance d'un fruit témoin, la conductivité hydraulique du phloème pourrait être alors estimée.

L'étude du paramètre d'extensibilité des parois a mis en évidence la possibilité d'une décroissance de ce paramètre vers la fin du développement du fruit, quand sa croissance ralentit, ce qui est cohérent avec la littérature. Les propriétés mécaniques des parois (extension ou ramollissement) sont sensibles à des variations du pH et à des acides, comme l'auxine qui pourrait induire l'extension des parois et donc une croissance (Okamoto *et al.*, 1990). (Mingo *et al.*, 2003) suggèrent que des signaux chimiques, tel que le pH, pourraient

jouer un rôle dans la régulation de l'expansion des cellules du fruit lors d'un stress hydrique. Des études ont montré que des expansines (McQueen-Mason, 1995), des endotransglycosidases (XET) et des peroxidases (Thompson *et al.*, 1998) joueraient un rôle dans les changements des structures des parois qui se déclenchent dans la phase finale de la croissance du fruit. L'activité des péroxidases a été particulièrement mise en évidence dans les parois de la peau juste avant le ralentissement de la croissance chez la tomate (Thompson *et al.*, 1998). Il apparaît alors très intéressant de pouvoir faire le lien entre l'arrêt de croissance, l'extensibilité des parois, et des changements de la physiologie du fruit, en mettant en place des travaux avec des physiologistes sur les variations de pH et de structure des parois, et avec des spécialistes en biologie moléculaire sur l'étude de ces enzymes clés.

Les résultats du modèle global de croissance en matière fraîche et de prédiction de la qualité du fruit à une date de récolte correspondant à la maturité sont globalement satisfaisants. Toutefois, ces résultats montrent des limites lors de la prédiction de la dynamique des critères de qualité et également lors de la généralisation du modèle aux différentes années d'expérimentation. On voit ici les limites d'une approche purement statistique pour modéliser l'accumulation des sucres et des acides. Une approche alternative serait de mieux comprendre les mécanismes et les enzymes impliqués dans l'élaboration de la qualité de la mangue. Ce type d'approche plus mécaniste a permis de modéliser l'accumulation des sucres (Génard *et al.*, 2003; Génard and Souty, 1996) et des acides (Lobit *et al.*, 2003) dans la pêche et semble avoir une meilleure qualité prédictive.

Un autre aspect important de l'élaboration de la qualité et peu abordé dans ce travail est le processus de maturation du fruit. Il est envisagé de poursuivre les travaux initiés en parallèle de mon travail de thèse (non présentés), en collaboration avec J. Joas (CIRAD Réunion) sur la maturation et son contrôle, en développant des travaux sur l'émission d'éthylène considérée comme une hormone importante de la maturation et sur la production des précurseurs de cette hormone au cours la croissance de la mangue (Morgan and Drew, 1997; Pech *et al.*, 1994). Nous pensons analyser ces processus en réponse à des variations du niveau d'alimentation carbonée, dont on connaît l'importance sur la maturité des fruits (Souty *et al.*, 1999). Ces expérimentations devraient nous servir de base pour développer par une approche mécaniste un travail de modélisation sur cette partie du développement du fruit.

2.2 Application de l'approche de modélisation

Le modèle que nous avons développé est un outil intéressant pour analyser la variabilité génétique de la qualité de la mangue. Notre étude a montré que la variation des paramètres liés à la respiration et à la mobilisation des réserves ne jouait que faiblement sur la qualité et que donc leur variabilité génétique n'a probablement que peu d'impact. Par contre, il est nécessaire d'avoir une bonne estimation, à partir d'expérimentations sur les génotypes

étudiées, des paramètres liés à la production d'assimilats carbonés par la photosynthèse foliaire et ceux liés à la demande du fruit. L'analyse de sensibilité du modèle de fonctionnement hydrique du fruit présentée dans le Chapitre IV à montré que ce modèle était principalement sensible aux paramètres liés à la plasticité et l'élasticité des parois qu'il serait judicieux d'étudier leur variation génotypique. Si la variation génotypique des paramètres est importante, on pourrait envisager la recherche des QTLs (Quantitative Trait Loci) de ces paramètres en vue d'une application pour la sélection variétale comme cela a été proposé sur la pêche par (Quilot, 2003).

L'application agronomique de mon travail est un point important qui concerne l'objectif de la maîtrise au champ de la qualité de la mangue. La réponse à cet objectif passe par l'optimisation des pratiques culturales.

Dans son état actuel, le modèle développé peut être utilisé pour rendre compte des variations des caractéristiques de la récolte (masse fraîche du fruit, qualité gustative à partir des saveurs sucrée et acide, teneur en matière sèche et concentrations en calcium pour les indicateurs de la durée de conservation) en réponse aux pratiques culturales affectant la disponibilité carbonée (charge en fruits) et hydrique (irrigation) et aux facteurs climatiques. Ce genre d'analyse se rapproche des études virtuelles présentées dans le Chapitre IV. Pour prendre en compte un acte technique comme l'éclaircissage qui joue sur la charge en fruits, le lien entre le nombre de fruits sur l'arbre et le rapport feuilles/fruit moyen, qui est une donnée d'entrée du modèle, est direct. La variable d'entrée du modèle liée à l'irrigation est le potentiel hydrique du rameau. Le lien entre cette variable d'entrée et celle de pilotage utilisée par les arboriculteurs est à modéliser. Une variable de pilotage pouvant être les variations de diamètre de tiges déjà utilisées par les arboriculteurs pour piloter l'irrigation (Amiraux, 2003) et présentant un lien direct avec le potentiel hydrique du rameau (Génard *et al.*, 2001). L'indicateur tensiométrique est également bien utilisé mais ici un modèle reliant cet indicateur et le potentiel hydrique du rameau serait à construire.

L'extension de notre modèle à l'arbre permettrait d'analyser l'effet des pratiques culturales sur la variabilité de la qualité dans la plante, ce qui serait une avancée très importante en matière de maîtrise de la qualité.

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Abstract

In this work, the effects of water and assimilate supplies on processes involved in mango fruit quality were investigated, in order to contribute to understand the intra-crown heterogeneity of mango fruit quality.

By an experimental approach, a strong link was found between water and carbon accumulation in each fruit component (peel, pulp and stone) regardless of treatments. The pulp is the component for which the size increased the most with the leaf-to-fruit ratio. Fresh mass and dry matter content are the main quality traits affected by assimilate supply in mango. Calcium, malic and citric acids, and fructose concentrations were higher, and those of sucrose were lower in fruits from treatment with the lowest assimilate supply. In our conditions, water supply affected weakly mango fruit quality.

The effects of assimilate supply on source/sink balance at the shoot bearing fruit level was analysed by experiments and models. The model computed processes as leaf photosynthesis, maintenance and growth respiration, reserves storage and mobilisation in leaves and stem, and fruit growth. Simulations using various climatic conditions were used to assess the respective contribution of climate changes, initial fruit dry mass and leaf-to-fruit ratio on processes involved in fruit growth.
Plant and fruit relations (water potential, turgor and osmotic pressures) and diurnal fruit growth were determined for studying and modelling reversible and irreversible enlargement processes in mango. The model simulates changes in elastic and plastic fruit growth under various assimilate supplies, with a set of parameters, as the elastic modulus, the cell wall extensibility and the yield threshold pressure which may change during the growth in mango, as we proposed in the model. Simulations in shortage of water or assimilate supply were analysed to study how it affects fruit water relations and fruit composition and the consequences on fruit fresh mass.

Those models were integrated in a global model which predicts at harvest fruit quality traits, like fruit fresh mass, dry matter content, and the main non structural compounds involved in sourness, sweetness, and shelf life. Simulations have shown that early fruit size affects positively fruit growth. Increased early fruit size improves eating quality at harvest (sweetness, sourness) but reduces quality aspects linked to shelf life.
Further studies are suggested in order to generalize this ecophysiological approach at the tree level and to the application of our global model to genetic variability analysis of mango fruit quality or to propose practical consequences of this work.

Key words: leaf-to-fruit ratio, irrigation, fruit growth and quality, simulation, water and dry matter linkage, mango fruit.

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Résumé

Dans ce travail, l'effet de la disponibilité hydrique et carbonée sur les processus impliqués dans l'élaboration de la qualité de la mangue a été étudié, afin de contribuer à expliquer la forte variabilité de la qualité de ce fruit au sein d'un même arbre.

Par une approche descriptive, un couplage fort entre l'accumulation de l'eau et de la matière sèche dans chaque compartiment de la mangue (peau, pulpe et noyau) à été mis en évidence. Il est apparu que la pulpe est le compartiment qui augmente le plus avec le rapport feuilles/fruit. Nous avons montré que la masse fraîche et la teneur en matière sèche de la pulpe sont les principaux critères de qualité influencés par l'alimentation carbonée. Les concentrations en calcium, en acides malique et citrique, et en fructose sont plus élevées, celles en saccharose plus faibles, dans les fruits en condition d'alimentation carbonée limitante que dans les fruits en condition non limitante. Dans nos conditions, la disponibilité hydrique n'a eu qu'un faible impact sur la qualité des mangues.

L'effet de la disponibilité carbonée sur les relations sources/puits au niveau du rameau fructifère a été étudié expérimentalement puis modélisé. Le modèle intègre les processus de photosynthèse, de respiration d'entretien et de croissance, de mise en réserves dans les feuilles et le bois, et de croissance du fruit. Ce modèle a permis de simuler, au cours d'une étude virtuelle sur deux sites à La Réunion et sept années successives, les processus impliqués dans le fonctionnement carboné du manguier et de quantifier l'effet du climat, de la taille initiale du fruit et du rapport feuilles/fruit sur chacun des processus.
La détermination de l'état hydrique des tissus de pulpe de mangue (pression de turgescence et osmotique) et des variations horaires de croissance du fruit ont permis d'étudier et de modéliser le fonctionnement hydrique de la mangue. Le modèle rend compte des variations de croissance réversible et irréversible grâce à l'introduction de variables liées aux propriétés d'élasticité et de plasticité des tissus. Des lois de variations de ces variables sont proposées pour la mangue. Une étude virtuelle montre comment les relations hydriques et la composition du fruit sont modifiées par les variations de la disponibilité carbonée et hydrique et quelles en sont les conséquences sur la croissance en masse fraîche du fruit.

Les modèles de fonctionnement carboné et hydrique ont été intégrés dans un modèle global de prédiction d'un profil de qualité comprenant la masse fraîche, la teneur en matière sèche, et les concentrations des principaux composés biochimiques et minéraux impliqués dans les saveurs sucrée et acide et liés à la conservation du fruit. L'étude virtuelle a mis en évidence l'effet positif de la masse initiale du fruit sur la croissance en matière fraîche. La masse initiale du fruit améliore également des critères de qualité gustative (saveurs sucrée et acide) à la récolte, mais en réduisant des indicateurs de la durée de conservation du fruit (teneur en matière sèche et concentration en calcium).
Des pistes de recherche sont proposées en vue d'une généralisation de l'analyse écophysiologique à l'échelle de l'arbre et d'une application du modèle global à l'analyse de la variabilité génétique de la qualité de la mangue ou à l'agronomie.

Mots clés: rapport feuilles/fruit, irrigation, croissance et qualité du fruit, modèle, couplage eau/carbone, mangue.

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